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# Heterosis and recombination effects on pig growth and carcass traits

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**ABSTRACT:** The primary objective was to estimate breed, heterosis, and recombination effects on growth and carcass traits of two different four-breed composite populations of pigs. Experiment 1 (Exp. 1) included purebred and crossbred pigs originating from Yorkshire, Landrace, Large White, and Chester White breeds, and Experiment 2 (Exp. 2) included pigs from Duroc, Hampshire, Pietrain, and Spot breeds. Data were recorded on purebred pigs, two-breed cross pigs, and pigs from generations $F_1$ through $F_6$, where $F_1$ pigs were the first generation of a four-breed cross. Pig weights were recorded at birth and at 14, 28, 56, 70, and 154 d of age. Average daily gain was calculated for intervals between weights, and ultrasonic backfat measurements (A-mode) were taken at 154 d of age. Feed intake was measured between 70 and 154 d of age on mixed pens of boars and barrows. Carcass backfat, length, and loin muscle area were measured on barrows at slaughter. Mixed-model analyses were done separately by experiment, fitting an animal model. Fixed effects included farrowing group and sex for growth traits and farrowing group for carcass traits. For ADFI, a weighted mixed-model analysis was done fitting farrowing group as a fixed effect, sire nested within farrowing group as a random effect, and weighting each observation by the number of pigs in each pen. To test feed efficiency, a second analysis of ADFI was done adding ADG as a covariate in the previous model. Included as covariates in all models were direct, maternal, and maternal grandam breed effects, direct and maternal heterosis effects, and a direct recombination effect. Recombination is the breakup of additive × additive epistatic effects present in purebreds during gamete formation by crossbred parents. Effects of direct heterosis significantly increased weights at birth, 14, 56, 70, and 154 d of age in Exp. 1. Effects of direct heterosis significantly increased ADG from birth to 14, 28 to 56, and 70 to 154 d of age in Exp. 1. In Exp. 2, effect of direct heterosis significantly increased weights and ADG at all ages. In Exp. 1, recombination significantly reduced loin muscle area. In Exp. 2, recombination significantly increased weights at birth, 14, 28, and 56 d, ADFI from 70 to 154 d, and ADFI adjusted for ADG. The correlation between maternal heterosis and recombination effects for all traits in Exp. 1 and Exp. 2 was approximately –0.90. Maternal heterosis and recombination effects were estimable, but greatly confounded.

Key Words: Correlation, Cytoplasm, Epistasis, Pigs, Recombination, Variance Components

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## Introduction

Characterization of breed, heterosis, and recombination effects is fundamental for efficient use of genetic resources in crossbreeding systems. These genetic effects may be expressed through direct (individual), paternal, maternal, and maternal grandam pathways. The optimal use of genetic resources and the comparative efficiency of different crossbreeding systems is determined by variation among breed effects relative to magnitudes of heterosis and recombination effects. However, few pig experiments have been designed to simultaneously estimate these genetic effects. In particular, estimates of recombination effects are scarce. Recombination loss, hereafter referred to as recombination, is the breakup of epistatic effects during meiosis to form nonparental interlocus combinations of alleles in gametes of crossbred parents (Dickerson, 1973). Recombination as defined by Dickerson (1973) included additive × additive effects only. Kinghorn (1983) demonstrated that a model including additive × additive effects adequately described epistatic effects associated with weight and tail length at 7 wk of age in crossbred mice.

In closed populations, epistatic effects may accumulate for traits under direct selection pressure, thereby improving performance of favorably correlated traits and diminishing performance of traits with antagonis-

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tic genetic correlations. Thus, epistatic effects on a specific trait may be either favorable or unfavorable depending on genetic relationships among traits and selection history of the population. If epistatic effects are relevant, then ignoring these effects will result in biased prediction of the performance of progeny from crossbred parents. If favorable epistatic effects exist for growth and carcass traits, then use of purebred boars as terminal sires may be preferable to use of crossbred boars.

The experimental objective was to estimate breed, heterosis, and recombination effects on growth and carcass traits of pigs.

## Materials and Methods

### General Experimental Design

*Population.* Young et al. (1986) described establishment of eight purebred populations which were utilized in this study. Matings were made during a 49-d breeding season. In Exp. 1, pigs derived from Yorkshire, Landrace, Large White, and Chester White breeds were born beginning in February each year. Experiment 2 pigs were born beginning in October of each year and included pigs derived from Duroc, Hampshire, Pietrain, and Spot breeds. About 125 litters were produced annually within each experiment. In 1980, two-breed crosses were produced using Chester White boars × Large White gilts and Yorkshire boars × Landrace gilts in Exp. 1 and reciprocal crosses of Duroc × Pietrain and Hampshire × Spot in Exp. 2. In 1981, the first generation of four-breed cross ($F_1$) pigs was produced using all possible combinations of available two-breed crosses. Each crossbred population was inter se mated thereafter, producing $F_2$, $F_3$, $F_4$, $F_5$, and $F_6$ litters in 1982, 1983, 1984, 1985, and 1986, respectively. Purebred pigs were produced contemporary to crossbred pigs from 1980 through 1984. In 1985, all possible two-breed crosses were produced contemporary to $F_5$ pigs within each experiment. In 1986, $F_6$ pigs were born contemporary to $F_1$ pigs created from all possible combinations of two-breed crosses. Year of birth, number of litters, and number of sires for each mating type in Exp. 1 and Exp. 2 are given in Table 1. Only data collected on pigs from first parity females were used. Thus, number of dams was equal to number of litters. Some purebred sires were used to produce both purebred and crossbred litters. Number of sires used to produce each mating type and total number used are given in Table 1.

*Management.* Pigs were reared by their own dams, except in a few cases (< 1%) when cross-fostering was allowed. Records collected on cross-fostered pigs before 70 d of age were excluded from analysis. Pigs were provided access to a commercial prestarter ration at 14 d of age. At 28 d of age, pigs were weaned, each litter was moved to a nursery pen, and pigs were provided ad libitum access to a corn-soybean meal diet that had a calculated ME of 3.28 Mcal/kg and a CP of 20.2%. At 56 d of age, two boars were randomly selected from each litter, and unselected males were castrated. At 63 d of age, pigs were moved from a nursery to a grower/finishing unit, and provided ad libitum access to a corn-soybean meal diet that had a calculated ME of 3.42 Mcal/kg and a CP of 17.3%. Approximately 75% of pigs were assigned to go on test from 70 to 154 d of age. Litters were selected for testing, such that, sires and breed-types were equally represented. Two boars and up to two barrows from each litter were placed together in a finishing pen. Gilts were grouped into finishing pens by breed type with 20 gilts per pen. Littermate gilts were normally grouped together.

*Data Collection.* Pigs were weighed at birth, 14, 28, 56, 70, and 154 d of age. For each interval between weights, ADG was calculated. At 154 d of age, backfat was measured at first rib, last rib, and last lumbar with an A-mode ultrasonic backfat machine (Scanogram Model 722; Ithaco Inc., Ithaca, NY). Backfat measurements were averaged across locations for analysis. A preliminary analysis was done to determine appropriate adjustment factors for average ultrasonic backfat. Ultrasonic backfat was adjusted to 80 kg live weight using linear and quadratic regression coefficients appropriate for sex and breed type. Barrows were slaughtered at a live weight of approximately 100 kg, and hot carcass weight, carcass length, loin muscle area, and carcass backfat at first rib, last rib, and last lumbar vertebra were recorded. Carcass backfat measurements were averaged across locations for analysis. Feed intake was recorded on pens of boars and barrows from 70 to 154 d of age.

*Statistical Analysis.* Genetic expectations are given in Table 2 for each mating type of Exp. 2 considering direct, maternal, paternal, and maternal grandam breed effects; direct, maternal, and paternal heterosis effects; and direct, maternal, and paternal recombination effects. Genetic expectations of $F_3$ and subsequent generations were assumed equivalent. The full genetic model for Exp. 1 was identical to that of Exp. 2 with exception of the breeds included. Estimable functions are illustrated in Table 3. Direct, maternal, and maternal grandam breed effects are reported as deviations from Yorkshire in Exp. 1 and from Duroc in Exp. 2. Direct and maternal heterosis effects are expressed as a percentage of the purebred mean. To calculate percentage heterosis, estimated effects were divided by an average of least-squares means of appropriate purebreds (Appendices 1 through 6). In appendices, progeny of reciprocal two-breed cross dams were classified separately to maintain breed identity of the maternal grandam. However, progeny of reciprocal two-breed cross sires were pooled as paternal effects were ignored.

Genetic parameters were estimated using the MTDFREML programs described by Boldman et al. (1995). All known pedigree relationships back to grandparents of 1980-born litters were included. Data were analyzed fitting effects of estimable functions as linear covariates (Robison et al., 1981). Multiple regression

**Table 1**. Year of birth, number of litters, and number of sires for each mating type in Experiments 1 and 2

| Experiment 1 | | | | Experiment 2 | | | |
|---|---|---|---|---|---|---|---|
| Mating type[a] | Year[b] | Litters | Sires[c] | Mating type[d] | Year[b] | Litters | Sires[c] |
| Purebreds | | | | | | | |
| Y × Y | 1980 to 1984 | 102 | 43 | H × H | 1980 to 1984 | 97 | 44 |
| L × L | 1980 to 1984 | 105 | 44 | D × D | 1980 to 1984 | 88 | 43 |
| W × W | 1980 to 1984 | 100 | 41 | P × P | 1980 to 1984 | 98 | 43 |
| C × C | 1980 to 1984 | 84 | 39 | S × S | 1980 to 1984 | 98 | 45 |
| Two-breed crosses | | | | | | | |
| Y × L | 1980, 1985 | 26 | 18 | H × D | 1985 | 6 | 6 |
| L × Y | 1985 | 5 | 5 | D × H | 1985 | 5 | 4 |
| Y × W | 1985 | 5 | 5 | P × S | 1985 | 6 | 5 |
| W × Y | 1985 | 5 | 4 | S × P | 1985 | 6 | 5 |
| L × W | 1985 | 5 | 5 | S × H | 1980, 1985 | 13 | 10 |
| W × L | 1985 | 5 | 5 | H × S | 1980, 1985 | 18 | 10 |
| W × C | 1985 | 4 | 4 | S × D | 1985 | 6 | 5 |
| C × L | 1985 | 5 | 4 | D × S | 1985 | 6 | 5 |
| L × C | 1985 | 5 | 5 | P × D | 1980, 1985 | 19 | 11 |
| C × Y | 1985 | 6 | 6 | D × P | 1980, 1985 | 15 | 8 |
| Y × C | 1985 | 5 | 5 | P × H | 1985 | 5 | 4 |
| C × W | 1980, 1985 | 27 | 12 | H × P | 1985 | 5 | 5 |
| Four-breed crosses | | | | | | | |
| $F_1$ | 1981, 1986 | 107 | 57 | $F_1$ | 1981, 1986 | 100 | 58 |
| $F_2$ | 1982 | 32 | 9 | $F_2$ | 1982 | 36 | 8 |
| $F_3$ | 1983 to 1986 | 235 | 78 | $F_3$ | 1983 to 1986 | 238 | 71 |
| Total | | 868 | 348[e] | | | 865 | 345[e] |

[a]Y = Yorkshire, L = Landrace, W = Large White, and C = Chester White. The first letter indicates breed of sire and the second letter indicates breed of dam. $F_3$, $F_4$, $F_5$, and $F_6$ were pooled.
[b]Year in which pigs were born.
[c]Some purebred sires were used to produce both purebred and crossbred litters.
[d]H = Hampshire, D = Duroc, P = Pietrain, and S = Spot. The first letter indicates breed of sire, and the second letter indicates breed of dam. $F_3$, $F_4$, $F_5$, and $F_6$ were pooled.
[e]Total number of sires used in this project. This number was not equal to the total of the column. The difference was due to sires producing both purebred and crossbred litters.

was preferable to linear contrasts among mating types because multiple regression coefficients provide a simultaneous weighting of all data as it exists (Koch et al., 1985). The full animal model included random animal genetic, maternal genetic, and common environment (litter of birth) effects. Maternal genetic and common environment effects were tested separately by comparing −2 residual log likelihoods of full and reduced (excluding the random effect of interest) models. The model which best fit the data was selected. Fixed effects of farrowing group and regression covariates were included in all models. In addition, fixed effect of sex was included when data from more than one sex were analyzed. Hot carcass weight, which averaged 76.8 kg in Exp. 1 and 76.5 kg in Exp. 2, was included as a linear regression covariate for analyzing carcass backfat, carcass length, and loin muscle area.

General form of the model was:

$$\mathbf{y} = \mathbf{X}\beta + \mathbf{Z_1u} + \mathbf{Z_2m} + \mathbf{Z_3c} + \mathbf{e}$$

where $\mathbf{y}$ was a vector of observations for a given trait; $\beta$, $\mathbf{u}$, $\mathbf{m}$, $\mathbf{c}$, and $\mathbf{e}$ are vectors of fixed, animal, maternal genetic, common environment, and residual effects, respectively; and $\mathbf{X}$, $\mathbf{Z_1}$, $\mathbf{Z_2}$, and $\mathbf{Z_3}$ are known design matrices. Expectations and (co)variances of random variables are:

$$\mathbf{E}\begin{bmatrix} u \\ m \\ c \\ e \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}$$

$$\mathbf{V}\begin{bmatrix} u \\ m \\ c \\ e \end{bmatrix} = \begin{bmatrix} \sigma^2_a A & \sigma_{am} A & 0 & 0 \\ \sigma_{am} A & \sigma^2_m A & 0 & 0 \\ 0 & 0 & \sigma^2_c I & 0 \\ 0 & 0 & 0 & \sigma^2_e I \end{bmatrix}$$

where $\sigma^2{}_a$, $\sigma^2{}_m$, $\sigma^2{}_c$, and $\sigma^2{}_e$ are additive genetic, maternal genetic, common environment, and residual variances, respectively, and $\sigma_{am}$ is the covariance between additive and maternal genetic effects. Matrices A and I represent numerator relationship and identity matrices, respectively.

Average daily feed intake was collected on a pen basis, and a weighted analysis was done using Proc Mixed in SAS (SAS Inst. Inc., Cary, NC). The model for ADFI included fixed effect of farrowing group, random effect of sire within farrowing group, and data were weighted

**Table 2**. Genetic expectation for each mating type in Experiment 2

| | Full genetic model[a] | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mating type | MU | $g_H^I$ | $g_P^I$ | $g_S^I$ | $g_D^I$ | $g_H^M$ | $g_P^M$ | $g_S^M$ | $g_D^M$ | $g_H^P$ | $g_P^P$ | $g_S^P$ | $g_D^P$ | $g_H^{MG}$ | $g_P^{MG}$ | $g_S^{MG}$ | $g_D^{MG}$ | $h^1$ | $h^M$ | $h^P$ | $r^1$ | $r^M$ | $r^P$ |
| D × D | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| H × H | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| P × P | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S × S | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| H × D | 1 | 0.5 | 0 | 0 | 0.5 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| D × H | 1 | 0.5 | 0 | 0 | 0.5 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| P × D | 1 | 0 | 0.5 | 0 | 0.5 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| D × P | 1 | 0 | 0.5 | 0 | 0.5 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| S × D | 1 | 0 | 0 | 0.5 | 0.5 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| D × S | 1 | 0 | 0 | 0.5 | 0.5 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| P × H | 1 | 0.5 | 0.5 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| H × P | 1 | 0.5 | 0.5 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| S × H | 1 | 0.5 | 0 | 0.5 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| H × S | 1 | 0.5 | 0 | 0.5 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| S × P | 1 | 0 | 0.5 | 0.5 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| P × S | 1 | 0 | 0.5 | 0.5 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| HD × PS | 1 | 0.25 | 0.25 | 0.25 | 0.25 | 0 | 0.5 | 0.5 | 0 | 0.5 | 0 | 0 | 0.5 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0.5 | 0 | 0 |
| HD × SP | 1 | 0.25 | 0.25 | 0.25 | 0.25 | 0 | 0.5 | 0.5 | 0 | 0.5 | 0 | 0 | 0.5 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0.5 | 0 | 0 |
| PD × HS | 1 | 0.25 | 0.25 | 0.25 | 0.25 | 0.5 | 0 | 0.5 | 0 | 0 | 0.5 | 0 | 0.5 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0.5 | 0 | 0 |
| PD × SH | 1 | 0.25 | 0.25 | 0.25 | 0.25 | 0.5 | 0 | 0.5 | 0 | 0 | 0.5 | 0 | 0.5 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0.5 | 0 | 0 |
| SD × HP | 1 | 0.25 | 0.25 | 0.25 | 0.25 | 0.5 | 0.5 | 0 | 0 | 0 | 0 | 0.5 | 0.5 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0.5 | 0 | 0 |
| SD × PH | 1 | 0.25 | 0.25 | 0.25 | 0.25 | 0.5 | 0.5 | 0 | 0 | 0 | 0 | 0.5 | 0.5 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0.5 | 0 | 0 |
| PH × DS | 1 | 0.25 | 0.25 | 0.25 | 0.25 | 0 | 0 | 0.5 | 0.5 | 0.5 | 0.5 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0.5 | 0 | 0 |
| PH × SD | 1 | 0.25 | 0.25 | 0.25 | 0.25 | 0 | 0 | 0.5 | 0.5 | 0.5 | 0.5 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0.5 | 0 | 0 |
| SH × DP | 1 | 0.25 | 0.25 | 0.25 | 0.25 | 0 | 0.5 | 0 | 0.5 | 0.5 | 0 | 0.5 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0.5 | 0 | 0 |
| SH × PD | 1 | 0.25 | 0.25 | 0.25 | 0.25 | 0 | 0.5 | 0 | 0.5 | 0.5 | 0 | 0.5 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0.5 | 0 | 0 |
| SP × DH | 1 | 0.25 | 0.25 | 0.25 | 0.25 | 0.5 | 0 | 0 | 0.5 | 0 | 0.5 | 0.5 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0.5 | 0 | 0 |
| SP × HD | 1 | 0.25 | 0.25 | 0.25 | 0.25 | 0.5 | 0 | 0 | 0.5 | 0 | 0.5 | 0.5 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0.5 | 0 | 0 |
| $F_2$ | 1 | 0.25 | 0.25 | 0.25 | 0.25 | 0.25 | 0.25 | 0.25 | 0.25 | 0.25 | 0.25 | 0.25 | 0.25 | 0.25 | 0.25 | 0.25 | 0.25 | 0.75 | 1 | 1 | 0.75 | 0.5 | 0.5 |
| $F_3$ | 1 | 0.25 | 0.25 | 0.25 | 0.25 | 0.25 | 0.25 | 0.25 | 0.25 | 0.25 | 0.25 | 0.25 | 0.25 | 0.25 | 0.25 | 0.25 | 0.25 | 0.75 | 0.75 | 0.75 | 0.75 | 0.75 | 0.75 |

[a] $g_i^I$, $g_i^M$, $g_i^P$, and $g_i^{MG}$ are direct, maternal, paternal, and maternal grandam breed effects. Subscript i represents a breed associated with the effect. D = Duroc, H = Hampshire, P = Pietrain, and S = Spot. $h^I$, $h^M$, and $h^P$ are direct, maternal, and paternal heterosis effects. $r^I$, $r^M$, and $r^P$ are direct, maternal, and paternal recombination effects. The first letter indicates breed of sire, and the second letter indicates breed of dam. Progeny of reciprocal two-breed dams were classified separately to account for maternal grandam breed effects, but progeny of reciprocal two-breed cross sires were pooled. Genetic expectations of $F_3$, $F_4$, $F_5$, and $F_6$ mating types were assumed equivalent.

**Table 3.** Estimable functions for Experiment 2

| Estimable function | Full genetic model[a] | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | MU | $g_H^I$ | $g_P^I$ | $g_S^I$ | $g_D^I$ | $g_H^M$ | $g_P^M$ | $g_S^M$ | $g_D^M$ | $g_H^P$ | $g_P^P$ | $g_S^P$ | $g_D^P$ | $g_H^{MG}$ | $g_P^{MG}$ | $g_S^{MG}$ | $g_D^{MG}$ | $h^I$ | $h^M$ | $h^P$ | $r^I$ | $r^M$ | $r^P$ |
| MU | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| $g_H^{I'}$ | 0 | 1 | 0 | 0 | −1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | −2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| $g_P^{I'}$ | 0 | 0 | 1 | 0 | −1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | −2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| $g_S^{I'}$ | 0 | 0 | 0 | 1 | −1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | −2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| $g_H^{M'}$ | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | −1 | −1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| $g_P^{M'}$ | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | −1 | 0 | −1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| $g_S^{M'}$ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | −1 | 0 | 0 | −1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| $g_H^{MG'}$ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | −1 | 0 | 0 | 0 | 0 | 0 | 0 |
| $g_P^{MG'}$ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | −1 | 0 | 0 | 0 | 0 | 0 | 0 |
| $g_S^{MG'}$ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | −1 | 0 | 0 | 0 | 0 | 0 | 0 |
| $h^{I'}$ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| $h^{M'}$ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | −1 | −1 |
| $r^{I'}$ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 2 |

[a] $g_{gi}^I$, $g_{gi}^M$, $g_{gi}^P$, and $g_{gi}^{MG}$ are direct, maternal, paternal, and maternal grandam breed effects. Subscript i represents a breed associated with the effect. D = Duroc, H = Hampshire, P = Pietrain, and S = Spot. $h^I$, $h^M$, and $h^P$ are direct, maternal, and paternal heterosis effects. $r^I$, $r^M$, and $r^P$ are direct, maternal, and paternal recombination effects. $g_{gi}^{I'}$, $g_{gi}^{M'}$, and $g_{gi}^{MG'}$ are estimable functions for direct, maternal, and maternal grandam breed effects. $h^{I'}$ and $h^{M'}$ are estimable functions for direct and maternal heterosis effects. $r^{I'}$ is an estimable function for the recombination effect.

by number of pigs in each pen. Estimable functions described previously were included as linear covariates. To test feed efficiency, a second analysis was done for ADFI adding ADG as a linear covariate in the model.

In a separate analysis, cytoplasmic effects were estimated for each trait from data collected on pigs from generations $F_3$, $F_4$, $F_5$, and $F_6$ (composite pigs). Given the full model previously described, composite pigs have identical genetic expectations with exception of their source of cytoplasm (Table 2). In Exp. 1, composite pigs had either Landrace or Large White cytoplasm. In Exp. 2, composite pigs had either Duroc, Hampshire, Pietrain, or Spot cytoplasm. In Exp. 2, source of cytoplasm was not a significant source of variation for growth, ADG, or carcass traits. In Exp. 1, pigs with Large White cytoplasm were 0.3 kg heavier at birth ($P < 0.01$) and had 2.34 $mm^2$ greater loin muscle area ($P < 0.01$) than pigs with Landrace cytoplasm. Little evidence existed for additional significant cytoplasmic effects on growth and carcass traits, and these effects were not considered further.

## Results

The set of estimable functions defined in Table 3 is not unique. To obtain solutions, 10 genetic effects were deleted from the design matrix of the full genetic model: direct, maternal, and maternal grandam breed effects of Duroc, paternal breed effects of Duroc, Hampshire, Pietrain, and Spot, paternal heterosis effects, maternal recombination effects, and paternal recombination effects. Estimable functions of direct, maternal, and maternal grandam breed effects of Hampshire, Pietrain, and Spot are therefore effects of these breeds relative to Duroc. It seemed reasonable to delete equations for paternal effects (breed, heterosis, and recombination) as well as the maternal recombination effect. If these effects do indeed exist, expectations of solutions are given in Table 3 to facilitate interpretation of results. The same method was used to obtain solutions for data collected in Exp. 1, with deletion of equations for Yorkshire effects.

Number of observations, means, (co)variance components, and estimates of genetic parameters are in Table 4 for Exp. 1 and Table 5 for Exp. 2. Direct heritability for weight increased from birth to 154 d of age in Exp. 1 (0.06 to 0.32) and Exp. 2 (0.02 to 0.25). Direct heritability for ADG increased with age from 0.09 to 0.37 in Exp. 1 and 0.08 to 0.26 in Exp. 2. Stewart and Schinckel (1991) summarized literature estimates and reported a heritability of 0.30 for ADG. This value was in good agreement with estimates of 0.37 and 0.26 for heritability of ADG from 70 to 154 d in Exp. 1 and Exp. 2, respectively. Maternal genetic variance as a proportion of phenotypic variance decreased as pigs aged. Common environment was defined as litter of birth in all models. Littermates were penned together until 56 d of age. From 70 to 154 d of age, littermate gilts were penned together with other gilts from their breed type, and

**Table 4**. Number of pigs, mean, (co)variance components, and genetic parameters for Experiment 1[a]

| Item | n | $\bar{x}$ | $\sigma^2_p$ | $\sigma^2_g$ | $\sigma^2_m$ | $\sigma_{am}$ | $\sigma^2_c$ | $h^2$ | $m^2$ | $c^2$ |
|---|---|---|---|---|---|---|---|---|---|---|
| Weight, kg | | | | | | | | | | |
| Birth | 7,685 | 1.26 | 0.075 | 0.005 | 0.022 | –0.003 | 0.013 | 0.06 ± 0.04 | 0.29 ± 0.05 | 0.17 |
| 14 d | 6,352 | 3.49 | 0.588 | 0.047 | 0.174 | –0.053 | 0.134 | 0.08 ± 0.05 | 0.30 ± 0.06 | 0.23 |
| 28 d | 6,268 | 6.31 | 1.940 | 0.191 | 0.481 | –0.186 | 0.590 | 0.10 ± 0.05 | 0.25 ± 0.06 | 0.30 |
| 56 d | 6,186 | 14.42 | 8.380 | 1.588 | 0.992 | –0.638 | 2.360 | 0.19 ± 0.06 | 0.12 ± 0.05 | 0.28 |
| 70 d | 4,393 | 21.24 | 9.470 | 1.850 | 1.063 | –0.735 | 2.669 | 0.20 ± 0.07 | 0.11 ± 0.05 | 0.28 |
| 154 d | 4,349 | 84.06 | 64.651 | 20.646 | — | — | 10.166 | 0.32 ± 0.04 | — | 0.16 |
| ADG, g/d | | | | | | | | | | |
| Birth to 14 d | 6,352 | 156 | 2,047 | 183 | 475 | –131 | 506 | 0.09 ± 0.05 | 0.23 ± 0.05 | 0.25 |
| 14 to 28 d | 6,268 | 200 | 3,424 | 230 | 457 | –219 | 1,366 | 0.07 ± 0.05 | 0.13 ± 0.05 | 0.40 |
| 28 to 56 d | 6,186 | 289 | 5,267 | 1,277 | — | — | 1,308 | 0.24 ± 0.04 | — | 0.25 |
| 70 to 154 d | 4,350 | 754 | 5,986 | 2,239 | — | — | 3,178 | 0.37 ± 0.04 | — | 0.10 |
| ADFI, kg | 583 | 2.36 | | | | | | | | |
| Ultrasonic backfat, mm | 4,346 | 17.41 | 9.24 | 4.09 | — | — | 0.79 | 0.44 ± 0.04 | | 0.09 |
| Carcass backfat, mm | 874 | 36.35 | 19.19 | 12.20 | 4.31 | –6.29 | 1.90 | 0.64 ± 0.19 | 0.22 ± 0.13 | 0.10 |
| Carcass length, cm | 874 | 79.44 | 4.76 | 3.02 | — | — | — | 0.63 ± 0.10 | — | — |
| Loin muscle area, cm$^2$ | 873 | 31.84 | 16.61 | 10.44 | — | — | — | 0.63 ± 0.10 | — | — |

[a]n = number of observations, $\bar{x}$ = phenotypic mean, $\sigma^2_p$ = phenotypic variance corrected for fixed effects, $\sigma^2_a$ = genetic variance due to direct effects, $\sigma^2_m$ = genetic variance due to maternal effects, $\sigma_{am}$ = genetic covariance between direct and maternal effects, $\sigma^2_c$ = variance due to common environment of litter, $h^2$ = proportion of the phenotypic variance due to $\sigma^2_a$, $m^2$ = proportion of the phenotypic variance due to $\sigma^2_m$, and $c^2$ = proportion of the phenotypic variance due to $\sigma^2_c$.

**Table 5**. Number of pigs, mean, (co)variance components, and genetic parameters for Experiment 2[a]

| Item | n | $\bar{x}$ | $\sigma^2_p$ | $\sigma^2_a$ | $\sigma^2_m$ | $\sigma^f_{am}$ | $\sigma^2_c$ | $h^2$ | $m^2$ | $c^2$ |
|---|---|---|---|---|---|---|---|---|---|---|
| Weight, kg | | | | | | | | | | |
| Birth | 7,154 | 1.32 | 0.077 | 0.001 | 0.007 | 0.003 | 0.017 | 0.02 ± 0.04 | 0.09 ± 0.04 | 0.22 |
| 14 d | 5,479 | 3.35 | 0.613 | 0.040 | 0.106 | –0.015 | 0.160 | 0.07 ± 0.05 | 0.17 ± 0.06 | 0.26 |
| 28 d | 5,362 | 6.08 | 2.140 | 0.006 | 0.316 | 0.029 | 0.645 | 0.00 ± 0.04 | 0.15 ± 0.06 | 0.30 |
| 56 d | 5,307 | 12.58 | 8.144 | 0.544 | 0.803 | 0.291 | 1.749 | 0.07 ± 0.05 | 0.10 ± 0.05 | 0.21 |
| 70 d | 4,053 | 18.80 | 10.383 | 2.033 | — | — | 3.054 | 0.20 ± 0.04 | — | 0.29 |
| 154 d | 3,996 | 79.48 | 89.68 | 22.032 | — | — | 12.203 | 0.25 ± 0.04 | — | 0.14 |
| ADG, g/d | | | | | | | | | | |
| Birth to 14 | 5,479 | 142 | 2,235 | 186 | 357 | –44 | 556 | 0.08 ± 0.05 | 0.16 ± 0.05 | 0.25 |
| 14 to 28 d | 5,362 | 193 | 4,303 | 308 | 556 | 413 | 1,119 | 0.07 ± 0.05 | 0.13 ± 0.05 | 0.26 |
| 28 to 56 d | 5,307 | 231 | 4,886 | 787 | 184 | 264 | 870 | 0.16 ± 0.05 | 0.04 ± 0.04 | 0.18 |
| 70 to 154 d | 3,995 | 722 | 8,476 | 2,230 | — | — | 844 | 0.26 ± 0.04 | — | 0.10 |
| ADFI, kg | 561 | 2.39 | | | | | | | | |
| Ultrasonic backfat, mm | 3,972 | 18.76 | 9.29 | 5.04 | 0.60 | –0.62 | 0.42 | 0.54 ± 0.06 | 0.06 ± 0.03 | 0.05 |
| Carcass backfat, mm | 698 | 34.96 | 20.03 | 13.72 | 3.38 | –3.42 | — | 0.68 ± 0.19 | 0.17 ± 0.11 | — |
| Carcass length, cm | 698 | 76.61 | 5.34 | 3.37 | 1.06 | –1.15 | 0.68 | 0.63 ± 0.23 | 0.20 ± 0.14 | 0.13 |
| Loin muscle area, cm$^2$ | 698 | 35.12 | 22.16 | 16.77 | — | — | — | 0.76 ± 0.11 | — | — |

[a]n = number of observations, $\bar{x}$ = phenotypic mean, $\sigma^2_p$ = phenotypic variance corrected for fixed effects, $\sigma^2_a$ = genetic variance due to direct effects, $\sigma^2_m$ = genetic variance due to maternal effects, $\sigma_{am}$ = genetic covariance between direct and maternal effects, $\sigma^2_c$ = variance due to common environment of litter, $h^2$ = proportion of the phenotypic variance due to $\sigma^2_a$, $m^2$ = proportion of the phenotypic variance due to $\sigma^2_m$, and $c^2$ = proportion of the phenotypic variance due to $\sigma^2_c$.

littermate boars and barrows were penned together. Including an effect due to common environment significantly improved model fit for all growth traits. Effect of common environment increased to weaning and declined thereafter. At young ages, direct heritability for growth was low relative to maternal heritability. This result is expected as pig growth at young ages is known to be influenced by litter size and milk production which are traits of the dam. Following weaning, direct heritability increased and maternal heritability declined as the genetic potential of the pig became relatively more important due to separation from its dam.

**Table 6**. Estimates and standard errors of estimable functions for weights (kg) in Experiment 1

| Estimable function[a] | Birth | 14 d | 28 d | 56 d | 70 d | 154 d |
|---|---|---|---|---|---|---|
| F-value | 0.77 | 1.03 | 1.32 | 0.04 | 0.07 | 0.54 |
| $g^{I'}_L$ | 0.08 ± 0.07 | 0.17 ± 0.22 | 0.01 ± 0.41 | 0.02 ± 0.89 | 0.22 ± 0.97 | 0.42 ± 2.39 |
| $g^{I'}_W$ | –0.02 ± 0.07 | –0.20 ± 0.22 | –0.50 ± 0.43 | 0.17 ± 0.90 | 0.42 ± 0.98 | 1.89 ± 2.29 |
| $g^{I'}_C$ | 0.04 ± 0.07 | 0.02 ± 0.21 | 0.34 ± 0.40 | 0.24 ± 0.86 | 0.08 ± 0.94 | –1.28 ± 2.32 |
| F-value | 2.20† | 4.05** | 3.99** | 1.14 | 0.75 | 2.98* |
| $g^{M'}_L$ | 0.20 ± 0.09 | –0.10 ± 0.28 | –0.15 ± 0.53 | 0.70 ± 1.01 | –0.06 ± 1.11 | –1.20 ± 2.22 |
| $g^{M'}_W$ | 0.09 ± 0.10 | 0.13 ± 0.29 | 0.43 ± 0.55 | 0.90 ± 1.01 | 0.44 ± 1.11 | 4.15 ± 2.17 |
| $g^{M'}_C$ | –0.03 ± 0.08 | –0.75 ± 0.26 | –1.30 ± 0.48 | –0.82 ± 0.88 | –1.10 ± 0.97 | –2.34 ± 1.89 |
| F-value | 1.20 | 2.03 | 0.99 | 0.48 | 0.47 | 2.11† |
| $g^{MG'}_L$ | 0.00 ± 0.07 | 0.22 ± 0.20 | 0.23 ± 0.38 | 0.04 ± 0.72 | 0.60 ± 0.80 | 3.26 ± 1.78 |
| $g^{MG'}_W$ | –0.04 ± 0.07 | 0.15 ± 0.20 | 0.10 ± 0.37 | –0.09 ± 0.72 | 0.10 ± 0.79 | –0.65 ± 1.80 |
| $g^{MG'}_C$ | 0.09 ± 0.07 | 0.47 ± 0.19 | 0.59 ± 0.36 | 0.67 ± 0.68 | 0.79 ± 0.76 | 1.65 ± 1.64 |
| $h^{I'}$ | 0.10 ± 0.03** | 0.23 ± 0.09* | 0.18 ± 0.18 | 1.46 ± 0.34*** | 2.57 ± 0.37*** | 7.15 ± 0.84*** |
| $h^{I'}$ % | 8.1 | 7.2 | 3.0 | 11.6 | 13.1 | 8.9 |
| $h^{M'}$ | 0.11 ± 0.08 | 0.17 ± 0.22 | 0.47 ± 0.40 | 0.16 ± 0.78 | –0.43 ± 0.86 | 0.04 ± 2.16 |
| $h^{M'}$ % | 8.9 | 5.3 | 7.9 | 1.3 | –2.2 | 0.0 |
| $r^{I'}$ | –0.09 ± 0.12 | 0.12 ± 0.32 | 0.11 ± 0.55 | 1.33 ± 1.13 | 1.68 ± 1.22 | 2.77 ± 3.53 |
| $h^{M'} + r^{I'}$ | 0.02 ± 0.06 | 0.29 ± 0.15† | 0.58 ± 0.27* | 1.49 ± 0.56** | 1.25 ± 0.61* | 2.81 ± 1.78 |

[a]$g^{I'}_i$, $g^{M'}_i$, and $g^{MG'}_i$ are estimable functions for direct, maternal, and maternal grandam breed effects. Subscript i represents a breed associated with the effect. L = Landrace, W = Large White, and C = Chester White. Direct, maternal, and maternal grandam breed effects for L, W, and C were estimated as deviations from Yorkshire breed effects. F-values are from a 3 degree of freedom F-test for direct, maternal, and maternal grandam breed effects. $h^{I'}$ and $h^{M'}$ are estimable functions for direct and maternal heterosis effects. $r^{I'}$ is an estimable function for the direct recombination effect.

†$P < 0.10$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

**Table 7**. Estimates and standard errors of estimable functions for weights (kg) in Experiment 2

| Estimable function[a] | Birth | 14 d | 28 d | 56 d | 70 d | 154 d |
|---|---|---|---|---|---|---|
| F-value | 1.69 | 0.96 | 0.64 | 3.39* | 4.44** | 9.00*** |
| $g_H^{I'}$ | 0.12 ± 0.06 | 0.30 ± 0.21 | 0.16 ± 0.35 | –0.51 ± 0.70 | –0.11 ± 0.98 | –1.02 ± 2.77 |
| $g_P^{I'}$ | 0.01 ± 0.06 | 0.00 ± 0.20 | –0.31 ± 0.34 | 0.27 ± 0.70 | –0.19 ± 0.97 | –8.56 ± 2.79 |
| $g_S^{I'}$ | 0.03 ± 0.06 | 0.18 ± 0.21 | –0.03 ± 0.35 | 1.69 ± 0.71 | 2.83 ± 0.98 | 5.58 ± 2.78 |
| F-value | 3.00* | 1.83 | 2.98* | 3.28* | 2.19† | 2.24† |
| $g_H^{M'}$ | –0.18 ± 0.08 | –0.07 ± 0.27 | 0.31 ± 0.50 | 0.26 ± 0.82 | 0.24 ± 0.93 | 1.18 ± 2.29 |
| $g_P^{M'}$ | –0.02 ± 0.08 | 0.21 ± 0.26 | 0.49 ± 0.48 | –0.28 ± 0.87 | 0.30 ± 0.91 | 2.91 ± 2.26 |
| $g_S^{M'}$ | 0.05 ± 0.08 | 0.53 ± 0.27 | 1.46 ± 0.51 | 2.25 ± 0.62 | 2.26 ± 0.96 | 5.95 ± 2.40 |
| F-value | 0.08 | 1.16 | 1.14 | 1.23 | 0.78 | 0.30 |
| $g_H^{MG'}$ | 0.02 ± 0.06 | –0.08 ± 0.18 | –0.03 ± 0.35 | –0.41 ± 0.62 | –0.96 ± 0.73 | –1.38 ± 1.84 |
| $g_P^{MG'}$ | –0.01 ± 0.06 | –0.16 ± 0.18 | –0.12 ± 0.34 | 0.03 ± 0.60 | –0.65 ± 0.70 | 0.20 ± 1.76 |
| $g_S^{MG'}$ | –0.01 ± 0.06 | –0.34 ± 0.19 | –0.60 ± 0.35 | –1.04 ± 0.63 | –0.93 ± 0.74 | –0.70 ± 1.85 |
| $h^{I'}$ | 0.12 ± 0.03*** | 0.51 ± 0.08*** | 0.83 ± 0.16*** | 2.26 ± 0.29*** | 3.36 ± 0.35*** | 11.04 ± 0.89*** |
| $h^{I'}$ % | 10.9 | 16.2 | 14.4 | 19.8 | 20.1 | 14.7 |
| $h^{M'}$ | –0.12 ± 0.07† | –0.48 ± 0.21 | –1.12 ± 0.39** | –1.53 ± 0.75* | –1.27 ± 0.85 | –2.27 ± 2.28 |
| $h^{M'}$ % | –10.9 | –15.2 | –19.5 | –13.4 | –7.6 | –3.0 |
| $r^{I'}$ | 0.19 ± 0.10† | 0.60 ± 0.31† | 1.16 ± 0.57* | 1.97 ± 1.16† | 1.80 ± 1.26 | 4.01 ± 3.64 |
| $h^{M'} + r^{I'}$ | 0.05 ± 0.05 | 0.12 ± 0.15 | 0.04 ± 0.28 | 0.44 ± 0.58 | 0.53 ± 0.64 | 1.74 ± 1.87 |

[a]$g_i^{I'}$, $g_i^{M'}$, and $g_i^{MG'}$ are estimable functions for direct, maternal, and maternal grandam breed effects. Subscript i represents a breed associated with the effect. H = Hampshire, P = Pietrain, and S = Spot. Direct, maternal, and maternal grandam breed effects for H, P, and S were estimated as deviations from Duroc breed effects. F-values are from a 3 degree of freedom F-test for direct, maternal, and maternal grandam breed effects. $h^{I'}$ and $h^{M'}$ are estimable functions for direct and maternal heterosis effects. $r^{I'}$ is an estimable function for the direct recombination effect.

†$P < 0.10$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

**Table 8**. Estimates and standard errors of estimable functions for ADG (g/d) in Experiment 1

| Estimable function[a] | Birth to 14 d | 14 to 28 d | 28 to 56 d | 70 to 154 d |
|---|---|---|---|---|
| F-value | 0.57 | 2.37† | 1.12 | 0.79 |
| $g_L^{I'}$ | 4 ± 13 | –15 ± 17 | –4 ± 21 | 5 ± 23 |
| $g_W^{I'}$ | –12 ± 13 | –25 ± 17 | 30 ± 20 | 22 ± 22 |
| $g_C^{I'}$ | –5 ± 12 | 20 ± 16 | 0 ± 20 | –14 ± 22 |
| F-value | 5.01** | 3.11* | 0.83 | 3.42* |
| $g_L^{M'}$ | –23 ± 16 | 0 ± 22 | 33 ± 21 | –8 ± 20 |
| $g_W^{M'}$ | 2 ± 17 | 28 ± 22 | 11 ± 18 | 47 ± 19 |
| $g_C^{M'}$ | –50 ± 15 | –39 ± 19 | 12 ± 16 | –12 ± 17 |
| F-value | 2.29† | 0.30 | 0.11 | 2.10† |
| $g_L^{MG'}$ | 18 ± 12 | 1 ± 16 | –7 ± 17 | 27 ± 16† |
| $g_W^{MG'}$ | 14 ± 12 | –6 ± 16 | –4 ± 17 | –10 ± 16 |
| $g_C^{MG'}$ | 29 ± 11 | 9 ± 15 | 2 ± 15 | 8 ± 15 |
| $h^{I'}$ | 10 ± 5* | –2 ± 7 | 44 ± 8*** | 54 ± 8*** |
| $h^{I'}$ % | 7.2 | –1.0 | 18.6 | 7.3 |
| $h^{M'}$ | 6 ± 13 | 23 ± 16 | –15 ± 19 | 8 ± 20 |
| $h^{M'}$ % | 4.3 | 11.7 | –6.4 | 1.1 |
| $r^{I'}$ | 12 ± 19 | –1 ± 20 | 50 ± 30† | 11 ± 34 |
| $h^{M'} + r^{I'}$ | 18 ± 9* | 22 ± 10* | 35 ± 15* | 19 ± 17 |

[a]$g_i^{I'}$, $g_i^{M'}$, and $g_i^{MG'}$ are estimable functions for direct, maternal, and maternal grandam breed effects. Subscript i represents a breed associated with the effect. L = Landrace, W = Large White, and C = Chester White. Direct, maternal, and maternal grandam breed effects for L, W, and C were estimated as deviations from Yorkshire breed effects. F-values are from a 3 degree of freedom F-test for direct, maternal, and maternal grandam breed effects. $h^{I'}$ and $h^{M'}$ are estimable functions for direct and maternal heterosis effects. $r^{I'}$ is an estimable function for the direct recombination effect.

†$P < 0.10$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

**Table 9**. Estimates and standard errors of estimable functions for ADG (g/d) in Experiment 2

| Estimable function[a] | Birth to 14 d | 14 to 28 d | 28 to 56 d | 70 to 154 d |
|---|---|---|---|---|
| F-value | 0.52 | 0.57 | 8.22*** | 9.51*** |
| $g_H^{I'}$ | 13 ± 13 | −7 ± 16 | −29 ± 19 | −6 ± 27 |
| $g_P^{I'}$ | 0 ± 13 | −21 ± 17 | 19 ± 19 | −96 ± 27 |
| $g_S^{I'}$ | 10 ± 13 | −13 ± 17 | 63 ± 19 | 41 ± 27 |
| F-value | 0.92 | 2.50† | 2.78* | 1.44 |
| $g_H^{M'}$ | 7 ± 16 | 23 ± 21 | 1 ± 18 | 8 ± 21 |
| $g_P^{M'}$ | 15 ± 15 | 18 ± 20 | −26 ± 18 | 28 ± 21 |
| $g_S^{M'}$ | 26 ± 16 | 57 ± 21 | 28 ± 19 | 42 ± 22 |
| F-value | 0.92 | 0.43 | 1.24 | 0.25 |
| $g_H^{MG'}$ | −5 ± 11 | 8 ± 16 | −15 ± 14 | −4 ± 17 |
| $g_P^{MG'}$ | −8 ± 11 | 3 ± 15 | 3 ± 14 | 10 ± 16 |
| $g_S^{MG'}$ | −18 ± 11 | −10 ± 16 | −20 ± 14 | 1 ± 17 |
| $h^{I'}$ | 28 ± 5*** | 26 ± 7*** | 53 ± 7*** | 88 ± 8*** |
| $h^{I'}$ % | 20.9 | 14.1 | 26.5 | 12.7 |
| $h^{M'}$ | −28 ± 13* | −50 ± 19** | −20 ± 18 | −7 ± 22 |
| $h^{M'}$ % | −20.9 | −27.1 | −10.0 | −1.0 |
| $r^{I'}$ | 33 ± 19† | 46 ± 31 | 36 ± 29 | 20 ± 35 |
| $h^{M'} + r^{I'}$ | 5 ± 9 | −4 ± 16 | 16 ± 15 | 13 ± 18 |

[a]$g_i^{I'}$, $g_i^{M'}$, and $g_i^{MG'}$ are estimable functions for direct, maternal, and maternal grandam breed effects. Subscript i represents a breed associated with the effect. H = Hampshire, P = Pietrain, and S = Spot. Direct, maternal, and maternal grandam breed effects for H, P, and S were estimated as deviations from Duroc breed effects. F-values are from a 3 degree of freedom F-test for direct, maternal, and maternal grandam breed effects. $h^{I'}$ and $h^{M'}$ are estimable functions for direct and maternal heterosis effects. $r^{I'}$ is an estimable function for the direct recombination effect.

†$P < 0.10$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Direct heritability estimates for ultrasonic backfat were 0.44 in Exp. 1 and 0.54 in Exp. 2. Stewart and Schinckel (1991) reviewed a number of studies and reported a weighted average of 0.41 for heritability of backfat. This value was reasonably consistent with estimates of ultrasonic backfat heritability in Exp. 1 and Exp. 2. Estimates of maternal and common environment effects were small relative to direct heritability for ultrasonic backfat. Heritability estimates of carcass length were similar in Exp. 1 and Exp. 2 and slightly greater than an estimate of 0.56 reported by Stewart and Schinckel (1991). Heritability estimates of average carcass backfat and loin muscle area in the present study were greater than those reported by Stewart and Schinckel (1991) for 10th rib carcass backfat (0.52) and loin muscle area (0.47).

Estimates and standard errors of estimable functions for each trait in each experiment are in Tables 6 through 12. The last rows in Tables 6 through 12 illustrate the net effect of maternal heterosis and recombination. Estimates of maternal heterosis and recombination were generally of opposite sign. Coefficients of maternal heterosis and direct recombination (Table 2) were highly confounded. Thus, it was difficult to obtain precise estimates of their separate effects. However, summing estimates of maternal heterosis and recombination effects was a good approximation of their net effect. Due to a relatively large negative covariance, standard errors of net effects were lower than standard errors of maternal heterosis and recombination individually.

Direct breed effects on weight did not differ significantly at any age in Exp. 1 (Table 6). Maternal breed effects tended to differ for birth weight. Significant maternal breed effects were detected for weight at 14, 28, and 154 d of age in Exp. 1. Maternal grandam breed effects tended to differ at 154 d. Direct heterosis significantly increased weights at birth, 14, 56, 70, and 154 d. Estimates of maternal heterosis and recombination effects for weights were not different from zero in Exp. 1. However, the net effect of maternal heterosis and recombination significantly increased weights at 28, 56, and 70 d of age.

Direct breed effects on weight differed at 56, 70, and 154 d in Exp. 2 (Table 7). Maternal breed effects significantly differed for weights at birth, 28, and 56 d and tended to differ at 70 and 154 d. Maternal grandam breed effects did not significantly affect weights. Direct heterosis significantly increased weights at all ages. Percentage direct heterosis for weights ranged from 3.0 to 13.1% in Exp. 1 and from 10.9 to 20.1% in Exp. 2. Percentage direct heterosis was greater in Exp. 2 than in Exp. 1 at all ages. Maternal heterosis effects significantly decreased pig weights at 28 and 56 d of age in Exp. 2. Percentage maternal heterosis ranged from −19.5 to −10.9% at young ages in Exp. 2. Thus, in Exp.

2, improved growth at young ages due to direct heterosis expressed by crossbred pigs was offset when the dam was also crossbred. In Exp. 2, recombination effects tended to increase weights at birth, 14 and 56 d and significantly increased weights at 28 d of age. However, this advantage was not significant at later ages. The net effect of maternal heterosis and recombination on weight did not significantly differ from zero in Exp. 2.

Direct breed effects tended to differ for ADG from 14 to 28 d in Exp. 1 (Table 8). Maternal breed effects differed significantly for ADG from birth to 14 d, 14 to 28 d, and 70 to 154 d. Maternal grandam breed effects tended to differ for ADG from birth to 14 d and 70 to 154 d. Effect of direct heterosis significantly increased ADG from birth to 14 d, 28 to 56 d, and 70 to 154 d. Effect of recombination tended to increase ADG from 28 to 56 d. Net effect of recombination and maternal heterosis significantly increased ADG from birth to 56 d of age.

In Exp. 2, direct breed effects differed significantly for ADG during postweaning intervals (Table 9). Maternal breed effects tended to differ for ADG from 14 to 28 d and differed significantly from 28 to 56 d. Direct heterosis significantly increased ADG during each interval. Percentage direct heterosis ranged from –1.0 to 18.6% in Exp. 1 and 12.7 to 26.5% in Exp. 2. As with weight traits, percentage direct heterosis was greater in Exp. 2 than in Exp. 1 during all intervals. From birth to 28 d, ADG was significantly reduced by maternal heterosis in Exp. 2. Effect of recombination tended to increase ADG from birth to 14 d of age. As observed for weight traits, maternal heterosis and recombination effects were offsetting in Exp. 2.

Direct breed effects tended to differ for ADFI in Exp. 1 and differed significantly for ADFI and ADFI adjusted for ADG in Exp. 2 (Table 10). Maternal breed effects tended to differ for ADFI adjusted for ADG in Exp. 2. Effects of direct heterosis significantly increased ADFI and ADFI adjusted for ADG in Exp. 1 and Exp. 2. In Exp. 2, effects of maternal heterosis decreased ADFI adjusted for ADG. Recombination and net effect of maternal heterosis and recombination increased ADFI and ADFI adjusted for ADG in Exp. 2.

Direct breed effects differed significantly for loin muscle area in Exp. 1, ultrasonic backfat in Exp. 2, and carcass backfat and length in Exp. 1 and Exp. 2 (Tables 11 and 12). In Exp. 1, maternal breed effects differed for ultrasonic backfat, carcass backfat, and loin muscle area. Likewise, maternal breed effects differed significantly for ultrasonic backfat and loin muscle area and tended to differ for carcass backfat in Exp. 2. With exception of loin muscle area in Exp. 1, maternal grandam breed, direct heterosis, maternal heterosis, and recombination effects did not significantly affect carcass traits in either experiment. In Exp. 1, maternal heterosis increased and recombination decreased loin muscle area. Considering maternal heterosis and recombination jointly, loin muscle area was significantly reduced.

## Discussion

The goal of these experiments was to determine if composite populations were an efficient method of utilizing heterosis and breed resources. Due to reproductive rates of pigs, terminal crossbreeding systems have become standard for pig production. However, the current study provides an opportunity to evaluate importance of nonadditive effects. If recombination effects are significant, then predictions of crossbreeding performance, which do not consider recombination effects, may be biased. When these experiments were initiated, no published estimates of recombination effects in pigs existed. These experiments were designed based on the model described by Dickerson (1973). Dickerson (1973) stated that recombination effects were due to a breakup of epistatic effects during gamete production in crossbred parents. Thus, progeny from a cross of purebred parents of unrelated breeds express 100% of available heterosis, and epistatic effects are maintained. When a crossbred animal reproduces, epistatic effects are broken up due to recombination during gamete formation. If one or both parents are crossbred and parents are of unlike breeds, progeny would again express 100% of available heterosis. However, epistatic effects which existed in purebred animals have now been partially broken up. Dickerson's (1973) model assumes no linkage. Breakup of epistatic effects may be slowed by linkage.

Epistatic effects are often assumed to be favorable and recombination effects unfavorable. When referring to a trait undergoing selection, recombination would be expected to result in diminished performance. Favorable combinations of genes with epistatic effects develop because they enhance performance for a trait which is subjected to natural or applied selection pressure. However, other economically important traits may be genetically and antagonistically correlated with the selected trait. In this case, combinations of genes develop with epistatic effects which enhance performance for the selected trait and diminish performance of negatively correlated traits. Thus, epistatic effects that are favorable for one trait, but unfavorable for another may accumulate in purebreds. For this reason, recombination effects may be positive or negative. In the present study, recombination effects that decreased loin muscle area in Exp. 1 and increased growth, ADFI, and kilograms of feed per kilograms of gain in Exp. 2 were identified.

Expectations of the 12 estimable functions are in Table 2. It was also important to consider relationships among estimable functions. Functions may be estimable and yet, still be highly confounded. Cunningham and Connolly (1989) described an approach for designing crossbreeding experiments and discussed correlations among estimates of additive, maternal, heterotic, and epistatic effects. Sampling correlations among estimable functions for weight at 70 d of age in Exp. 2 are shown in Table 13. Sampling correlations for all traits

**Table 10**. Estimates and standard errors of estimable functions for ADFI (kg/d) and ADFI adjusted for ADG (kg/d) in Experiments 1 and 2

| Experiment 1 | | | Experiment 2 | | |
|---|---|---|---|---|---|
| Estimable function[a] | ADFI | ADFI adjusted for ADG | Estimable function[a] | ADFI | ADFI adjusted for ADG |
| F-value | 2.36† | 0.53 | F-value | 11.48*** | 9.81*** |
| $g_L^{I'}$ | 0.13 ± 0.10 | 0.02 ± 0.07 | $g_H^{I'}$ | −0.11 ± 0.13 | −0.22 ± 0.11 |
| $g_W^{I'}$ | 0.14 ± 0.10 | 0.06 ± 0.07 | $g_P^{I'}$ | −0.40 ± 0.13 | −0.21 ± 0.10 |
| $g_C^{I'}$ | −0.11 ± 0.10 | −0.03 ± 0.07 | $g_S^{I'}$ | 0.37 ± 0.13 | 0.28 ± 0.11 |
| F-value | 0.27 | 0.25 | F-value | 0.46 | 2.12† |
| $g_L^{M'}$ | −0.03 ± 0.14 | 0.05 ± 0.10 | $g_H^{M'}$ | −0.08 ± 0.16 | −0.12 ± 0.13 |
| $g_W^{M'}$ | 0.04 ± 0.13 | −0.03 ± 0.10 | $g_P^{M'}$ | −0.12 ± 0.16 | −0.18 ± 0.13 |
| $g_C^{M'}$ | −0.07 ± 0.12 | 0.02 ± 0.08 | $g_S^{M'}$ | −0.20 ± 0.18 | −0.36 ± 0.14 |
| F-value | 1.71 | 1.98 | F-value | 0.97 | 1.30 |
| $g_L^{MG'}$ | 0.04 ± 0.10 | −0.05 ± 0.07 | $g_H^{MG'}$ | 0.07 ± 0.12 | 0.16 ± 0.10 |
| $g_W^{MG'}$ | −0.04 ± 0.10 | −0.09 ± 0.07 | $g_P^{MG'}$ | 0.19 ± 0.12 | 0.15 ± 0.09 |
| $g_C^{MG'}$ | 0.17 ± 0.09 | 0.08 ± 0.07 | $g_S^{MG'}$ | 0.15 ± 0.12 | 0.16 ± 0.10 |
| $h^{I'}$ | 0.24 ± 0.05*** | 0.10 ± 0.04** | $h^{I'}$ | 0.45 ± 0.06*** | 0.16 ± 0.05** |
| $h^{I'}$ % | 10.8 | | $h^{I'}$ % | 21.1 | |
| $h^{M'}$ | 0.00 ± 0.10 | −0.07 ± 0.07 | $h^{M'}$ | −0.20 ± 0.13 | −0.21 ± 0.10* |
| $h^{M'}$ % | 0.0 | | $h^{M'}$ % | −9.4 | |
| $r^{I'}$ | 0.03 ± 0.10 | 0.03 ± 0.07 | $r^{I'}$ | 0.38 ± 0.13** | 0.36 ± 0.10*** |
| $h^{M'} + r^{I'}$ | 0.03 ± 0.05 | −0.04 ± 0.03 | $h^{M'} + r^{I'}$ | 0.18 ± 0.06** | 0.15 ± 0.05** |

[a] $g_i^{I'}$, $g_i^{M'}$, and $g_i^{MG'}$ are estimable functions for direct, maternal, and maternal grandam breed effects. Subscript i represents a breed associated with the effect. L = Landrace, W = Large White, C = Chester White, H = Hampshire, P = Pietrain, and S = Spot. Direct, maternal, and maternal grandam breed effects were estimated as deviations from the effect of Yorkshire in Experiment 1 and Duroc in Experiment 2. F-values are from a 3 degree of freedom F-test for direct, maternal, and maternal grandam breed effects. $h^{I'}$ and $h^{M'}$ are estimable functions for direct and maternal heterosis effects. $r^{I'}$ is an estimable function for the direct recombination effect.

†$P < 0.10$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

**Table 11**. Estimates and standard errors of estimable functions for carcass traits in Experiment 1

| Estimable function[a] | Ultrasonic backfat, mm | Carcass backfat, mm | Carcass length, cm | Loin muscle area, $cm^2$ |
|---|---|---|---|---|
| F-value | 0.17 | 3.89** | 4.60** | 3.09* |
| $g_L^{I'}$ | −0.34 ± 0.92 | −3.66 ± 2.15 | 2.78 ± 0.95 | −2.48 ± 1.76 |
| $g_W^{I'}$ | 0.29 ± 0.87 | 2.00 ± 2.18 | 0.85 ± 0.92 | −2.68 ± 1.73 |
| $g_C^{I'}$ | 0.09 ± 0.91 | −4.39 ± 2.17 | −0.73 ± 0.96 | 2.44 ± 1.82 |
| F-value | 6.83*** | 2.78* | 0.49 | 3.51* |
| $g_L^{M'}$ | 0.75 ± 0.75 | 0.64 ± 2.30 | 0.53 ± 0.94 | −1.56 ± 1.76 |
| $g_W^{M'}$ | −0.50 ± 0.73 | −1.78 ± 2.17 | 0.28 ± 0.87 | −0.37 ± 1.63 |
| $g_C^{M'}$ | 2.48 ± 0.62 | 4.42 ± 2.02 | −0.54 ± 0.81 | −4.60 ± 1.52 |
| F-value | 0.99 | 0.74 | 0.26 | 0.17 |
| $g_L^{MG'}$ | −0.43 ± 0.62 | −1.41 ± 1.58 | 0.54 ± 0.74 | 0.83 ± 1.39 |
| $g_W^{MG'}$ | 0.12 ± 0.62 | −2.09 ± 1.49 | 0.53 ± 0.72 | 0.47 ± 1.34 |
| $g_C^{MG'}$ | −0.80 ± 0.56 | −1.50 ± 1.44 | 0.48 ± 0.68 | 0.04 ± 1.27 |
| $h^{I'}$ | 0.32 ± 0.30 | 0.16 ± 0.77 | −0.04 ± 0.36 | 0.52 ± 0.68 |
| $h^{I'}$ % | 1.7 | 0.4 | −0.1 | 1.6 |
| $h^{M'}$ | 1.03 ± 0.79 | 0.53 ± 1.66 | −0.73 ± 0.92 | 4.30 ± 1.76* |
| $h^{M'}$ % | 5.6 | 1.5 | −0.9 | 13.6 |
| $r^{I'}$ | −1.86 ± 1.36 | −0.14 ± 2.29 | 0.76 ± 1.54 | −7.66 ± 2.88** |
| $h^{M'} + r^{I'}$ | −0.83 ± 0.69 | 0.39 ± 1.17 | 0.03 ± 0.78 | −3.36 ± 1.45* |

[a] $g_i^{I'}$, $g_i^{M'}$, and $g_i^{MG'}$ are estimable functions for direct, maternal, and maternal grandam breed effects. Subscript i represents a breed associated with the effect. L = Landrace, W = Large White, and C = Chester White. Direct, maternal, and maternal grandam breed effects for L, W, and C were estimated as deviations from Yorkshire breed effects. F-values are from a 3 degree of freedom F-test for direct, maternal, and maternal grandam breed effects. $h^{I'}$ and $h^{M'}$ are estimable functions for direct and maternal heterosis effects. $r^{I'}$ is an estimable function for the direct recombination effect.

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

**Table 12**. Estimates and standard errors of estimable functions for carcass traits in Experiment 2

| Estimable function[a] | Ultrasonic backfat, mm | Carcass backfat, mm | Carcass length, cm | Loin muscle area, cm$^2$ |
|---|---|---|---|---|
| F-value | 3.82** | 5.40** | 9.53*** | 1.31 |
| $g_H^{I'}$ | −3.74 ± 1.12 | −5.45 ± 2.39 | 1.58 ± 1.26 | 3.64 ± 2.38 |
| $g_P^{I'}$ | −1.46 ± 1.13 | 3.69 ± 2.41 | −3.89 ± 1.25 | 1.52 ± 2.43 |
| $g_S^{I'}$ | −1.32 ± 1.12 | 2.14 ± 2.46 | 1.88 ± 1.29 | −1.08 ± 2.49 |
| F-value | 8.41*** | 2.37† | 0.63 | 4.23** |
| $g_H^{M'}$ | 0.39 ± 0.76 | 1.57 ± 2.13 | −1.08 ± 1.17 | 0.21 ± 1.88 |
| $g_P^{M'}$ | −2.12 ± 0.76 | −3.73 ± 2.12 | −1.56 ± 1.16 | 5.70 ± 1.86 |
| $g_S^{M'}$ | −2.98 ± 0.79 | −1.83 ± 2.35 | −0.78 ± 1.28 | 2.10 ± 2.13 |
| F-value | 0.93 | 1.08 | 0.24 | 1.96 |
| $g_H^{MG'}$ | −0.23 ± 0.54 | −1.29 ± 1.48 | 0.28 ± 0.80 | 1.08 ± 1.53 |
| $g_P^{MG'}$ | 0.48 ± 0.53 | 0.41 ± 1.37 | 0.60 ± 0.74 | −1.55 ± 1.39 |
| $g_S^{MG'}$ | 0.58 ± 0.55 | −1.90 ± 1.53 | 0.17 ± 0.82 | 1.75 ± 1.56 |
| $h^{I'}$ | 0.11 ± 0.27 | −0.07 ± 0.84 | 0.73 ± 0.45 | 0.47 ± 0.86 |
| $h^{I'}$ % | 0.6 | −0.2 | 1.0 | 1.3 |
| $h^{M'}$ | 0.10 ± 0.74 | 0.77 ± 1.92 | −1.44 ± 1.00 | −0.54 ± 2.05 |
| $h^{M'}$ % | 0.5 | 2.2 | −1.9 | −1.5 |
| $r^{I'}$ | −0.20 ± 1.27 | −2.87 ± 2.91 | 1.18 ± 1.43 | 0.98 ± 3.33 |
| $h^{M'} + r^{I'}$ | −0.10 ± 0.66 | −2.10 ± 1.51 | −0.26 ± 0.74 | 0.44 ± 1.76 |

[a]$g_i^{I'}$, $g_i^{M'}$, and $g_i^{MG'}$ are estimable functions for direct, maternal, and maternal grandam breed effects. Subscript i represents a breed associated with the effect. H = Hampshire, P = Pietrain, and S = Spot. Direct, maternal, and maternal grandam breed effects for H, P, and S were estimated as deviations from Duroc breed effects. F-values are from a 3 degree of freedom F-test for direct, maternal, and maternal grandam breed effects. $h^{I'}$ and $h^{M'}$ are estimable functions for direct and maternal heterosis effects. $r^{I'}$ is an estimable function for the direct recombination effect.

†$P < 0.10$, **$P < 0.01$, ***$P < 0.001$.

in Exp. 1 were similar as were correlations in Exp. 2. As expected, sampling correlations of $g_i^I$ with $g_i^M$, were greater than those of $g_i^I$ with $g_j^M$. Thus, it was more difficult to separate direct and maternal effects within breeds than it was to separate the direct effect of breed i from maternal effect of breed j.

The correlation of greatest concern was between maternal heterosis and recombination, which averaged −0.90 across traits. A primary objective of this experiment was to estimate effects of recombination. However, maternal heterosis and recombination were highly correlated, and little opportunity existed to separate these effects. Including backcross matings would have provided additional opportunity to separate estimates of maternal heterosis and recombination. Summing maternal heterosis and recombination effects was a good approximation of their net effect. In a four-breed composite, 0.75 is the coefficient for both maternal het-

**Table 13**. Sampling correlations among estimable functions for weight at 70 d of age in Experiment 2[a]

| Estimable function | $g_H^{I'}$ | $g_P^{I'}$ | $g_S^{I'}$ | $g_H^{M'}$ | $g_P^{M'}$ | $g_S^{M'}$ | $g_H^{MG'}$ | $g_P^{MG'}$ | $g_S^{MG'}$ | $h^{I'}$ | $h^{M'}$ | $r^{I'}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| $g_H^{I'}$ | 1.00 | 0.51 | 0.48 | −0.43 | −0.21 | −0.22 | −0.08 | −0.03 | −0.01 | −0.02 | −0.03 | 0.03 |
| $g_P^{I'}$ | | 1.00 | 0.51 | −0.21 | −0.43 | −0.20 | −0.03 | −0.08 | −0.02 | −0.05 | 0.04 | −0.02 |
| $g_S^{I'}$ | | | 1.00 | −0.20 | −0.22 | −0.45 | −0.04 | −0.03 | −0.04 | −0.04 | −0.04 | 0.05 |
| $g_H^{M'}$ | | | | 1.00 | 0.48 | 0.44 | −0.70 | −0.35 | −0.32 | 0.04 | 0.00 | −0.03 |
| $g_P^{M'}$ | | | | | 1.00 | 0.47 | −0.34 | −0.71 | −0.34 | 0.04 | −0.01 | −0.02 |
| $g_S^{M'}$ | | | | | | 1.00 | −0.28 | −0.33 | −0.73 | 0.04 | 0.05 | −0.06 |
| $g_H^{MG'}$ | | | | | | | 1.00 | 0.48 | 0.42 | 0.00 | 0.04 | −0.01 |
| $g_P^{MG'}$ | | | | | | | | 1.00 | 0.47 | 0.00 | −0.03 | 0.04 |
| $g_S^{MG'}$ | | | | | | | | | 1.00 | 0.00 | −0.01 | 0.03 |
| $h^{I'}$ | | | | | | | | | | 1.00 | −0.38 | 0.14 |
| $h^{M'}$ | | | | | | | | | | | 1.00 | −0.89 |
| $r^{I'}$ | | | | | | | | | | | | 1.00 |

[a]$g_i^{I'}$, $g_i^{M'}$, and $g_i^{MG'}$ are estimable functions for direct, maternal, and maternal grandam breed effects. Subscript i represents a breed associated with the effect. H = Hampshire, P = Pietrain, and S = Spot. $h^{I'}$ and $h^{M'}$ are estimable functions for direct and maternal heterosis effects. $r^{I'}$ is an estimable function for the direct recombination effect.

erosis and recombination (Table 2). Thus, 0.75 × (maternal heterosis effect + recombination effect) was an approximation of the net effect of maternal heterosis and recombination in a four-breed composite.

Direct breed effects on growth differed significantly more often in Exp. 2 than Exp. 1. Heterosis effects on growth, when expressed as a percentage, were greater in Exp. 2 than Exp. 1. Because of common heritage of Yorkshire, Large White, and Chester White, greater genetic divergence was expected among Duroc, Hampshire, Pietrain, and Spot than among Yorkshire, Landrace, Large White, and Chester White.

Johnson (1980) summarized data from NC-103 cooperating stations estimating breed and heterosis effects. Direct breed effects differed significantly for growth and carcass traits. Direct heterosis effects were significant for growth traits and carcass backfat but not carcass length or loin muscle area. Present results were consistent with two exceptions. A significant effect of maternal heterosis on loin muscle area was detected in Exp. 1, and direct heterosis effects on carcass backfat were not detected. Baas et al. (1992) estimated heterosis and recombination effects on carcass traits of pigs. The population consisted of purebred Landrace and Hampshire pigs, reciprocal matings among purebreds, backcrosses, and $F_2$ and $F_3$ generations of inter-se matings among $F_1$ pigs. Baas et al. (1992) reported a decrease in carcass length due to direct recombination, an increase in carcass length due to maternal recombination, and an increase in tenth-rib carcass backfat due to direct recombination. No significant effects of recombination on carcass length or backfat were detected in the present study. A significant negative effect of recombination on loin muscle area was detected in Exp. 1 but not in Exp. 2. Baas et al. (1992) reported a negative effect of direct recombination on loin muscle area; however, the effect did not approach significance. Results of the present study may differ from those of Baas et al. (1992) for a number of reasons. The study of Baas et al. (1992) included pigs from Landrace and Hampshire breeds only. In addition, population structure differed between studies. Finally, the present study included eight breeds and more observations.

## Implications

Estimates of genetic effects are useful to evaluate pig breeds and to develop efficient crossbreeding systems. Growth and carcass traits were influenced by breed of pig and dam, but seldom by breed of maternal grandam. Crossbred pigs grew more rapidly than purebred pigs, but differences between purebred and crossbred pigs were less important for carcass traits. Growth of young pigs raised by purebred or crossbred dams often differed. Relative to progeny of purebred parents, new allelic combinations among genes exist in progeny of crossbred sires and dams. These new combinations tended to increase growth, daily feed intake, and carcass length, while decreasing backfat. Loin muscle area was reduced by new combinations in one group of breeds, but not in another group. In general, crossbred sires and dams can be used in mating systems without concern for adverse effects of new genetic combinations. New combinations tended to produce neutral or favorable effects.

## Literature Cited


Baas, T. J., L. L. Christian, and M. F. Rothschild. 1992. Heterosis and recombination effects in Hampshire and Landrace swine: II. Performance and carcass traits. J. Anim. Sci. 70:99–105.

Boldman, K. G., L. A. Kriese, L. D. Van Vleck, C. P. Van Tassell, and S. D. Kachman. 1995. A manual for the use of MTDFREML. Agricultural Research Service, USDA, Clay Center, NE.

Cunningham, E. P., and J. Connolly. 1989. Efficient design of crossbreeding experiments. Theor. Appl. Genet. 78:381–386.

Dickerson, G. 1973. Inbreeding and heterosis in animals. In: Proc. of the Animal Breeding and Genetics Symp. in Honor of Dr. Jay L. Lush, Amer. Soc. Anim. Sci., Champaign, IL. pp 54–77.

Johnson, R. K. 1980. Heterosis and breed effects in swine. North Central Regional Publication No. 206. Nebraska Agricultural Experiment Station, Lincoln.

Kinghorn, G. 1983. Genetic effects in crossbreeding. III. Epistatic loss in crossbred mice. Z. Tierz. Züechtungsbiol. 100:209.

Koch, R. M., G. E. Dickerson, L. V. Cundiff, and K. E. Gregory. 1985. Heterosis retained in advanced generations of crosses among Angus and Hereford cattle. J. Anim. Sci. 60:1117–1132.

Robison, O. W., B. T. McDaniel, and E. J. Rincon. 1981. Estimation of direct and maternal additive and heterotic effects from crossbreeding experiments in animals. J. Anim. Sci. 52:44–50.

Stewart, T. S., and A. P. Schinckel. 1991. Genetic parameters for swine growth and carcass traits. In: L. D. Young (ed.) *Genetics of Swine*. p 77. USDA-ARS, Roman L. Hruska U.S. Meat Animal Research Center, Clay Center, NE.

Young, L. D., K. A. Leymaster, and D. D. Lunstra. 1986. Genetic variation in testicular development and its relationship to female reproductive traits in swine. J. Anim. Sci. 63:17–26.

# Appendix

**Appendix Table 1**. Least-squares means and standard errors of breed types for weights (kg) in Experiment 1

| Breed type[a] | Birth | 14 d | 28 d | 56 d | 70 d | 154 d |
|---|---|---|---|---|---|---|
| Y × Y | 1.13 ± 0.05 | 3.12 ± 0.13 | 5.94 ± 0.23 | 12.2 ± 0.5 | 19.3 ± 0.3 | 79.5 ± 0.6 |
| L × L | 1.44 ± 0.05 | 3.41 ± 0.13 | 6.06 ± 0.23 | 13.0 ± 0.5 | 20.2 ± 0.3 | 82.6 ± 0.6 |
| W × W | 1.18 ± 0.05 | 3.22 ± 0.13 | 6.05 ± 0.23 | 13.0 ± 0.5 | 20.0 ± 0.3 | 84.3 ± 0.7 |
| C × C | 1.19 ± 0.05 | 2.98 ± 0.13 | 5.77 ± 0.23 | 12.2 ± 0.5 | 19.0 ± 0.3 | 76.6 ± 0.7 |
| Y × L | 1.52 ± 0.06 | 3.63 ± 0.15 | 6.33 ± 0.28 | 14.3 ± 0.6 | 22.3 ± 0.5 | 88.2 ± 1.1 |
| L × Y | 1.22 ± 0.09 | 3.52 ± 0.25 | 6.56 ± 0.45 | 14.0 ± 0.9 | 21.8 ± 0.9 | 89.5 ± 2.2 |
| Y × W | 1.36 ± 0.09 | 4.15 ± 0.24 | 7.45 ± 0.44 | 14.8 ± 0.9 | 22.6 ± 0.9 | 89.4 ± 2.2 |
| W × Y | 1.27 ± 0.09 | 3.40 ± 0.26 | 6.09 ± 0.47 | 13.8 ± 0.9 | 22.2 ± 1.0 | 85.7 ± 2.3 |
| L × W | 1.46 ± 0.09 | 4.04 ± 0.25 | 7.34 ± 0.46 | 16.3 ± 0.9 | 23.7 ± 0.9 | 94.1 ± 2.3 |
| W × L | 1.49 ± 0.09 | 3.67 ± 0.25 | 6.61 ± 0.45 | 15.6 ± 0.9 | 23.0 ± 0.9 | 90.0 ± 2.2 |
| W × C | 1.39 ± 0.09 | 3.62 ± 0.25 | 6.29 ± 0.46 | 15.3 ± 0.9 | 23.3 ± 0.9 | 90.0 ± 2.3 |
| C × L | 1.48 ± 0.09 | 3.60 ± 0.25 | 6.89 ± 0.47 | 15.4 ± 0.9 | 23.2 ± 1.0 | 89.0 ± 2.3 |
| L × C | 1.27 ± 0.09 | 3.88 ± 0.24 | 6.82 ± 0.44 | 15.4 ± 0.9 | 22.8 ± 0.9 | 87.7 ± 2.2 |
| C × Y | 1.22 ± 0.08 | 3.70 ± 0.24 | 6.55 ± 0.44 | 14.2 ± 0.9 | 21.9 ± 0.9 | 85.5 ± 2.2 |
| Y × C | 1.23 ± 0.09 | 3.29 ± 0.29 | 6.15 ± 0.52 | 13.2 ± 1.1 | 21.8 ± 1.0 | 85.9 ± 2.5 |
| C × W | 1.30 ± 0.06 | 3.45 ± 0.17 | 6.42 ± 0.30 | 14.3 ± 0.6 | 22.1 ± 0.5 | 90.4 ± 1.2 |
| YL × CW | 1.30 ± 0.06 | 3.40 ± 0.16 | 6.25 ± 0.30 | 14.2 ± 0.6 | 22.1 ± 0.5 | 87.7 ± 1.3 |
| YL × WC | 1.44 ± 0.09 | 3.90 ± 0.25 | 6.98 ± 0.46 | 16.0 ± 0.9 | 23.1 ± 0.9 | 90.5 ± 2.2 |
| YW × CL | 1.45 ± 0.08 | 3.66 ± 0.23 | 6.53 ± 0.42 | 15.5 ± 0.9 | 22.7 ± 0.9 | 91.1 ± 2.1 |
| YW × LC | 1.47 ± 0.08 | 3.80 ± 0.22 | 6.95 ± 0.41 | 15.9 ± 0.8 | 23.3 ± 0.8 | 88.3 ± 2.0 |
| LW × CY | 1.28 ± 0.08 | 3.22 ± 0.23 | 5.85 ± 0.43 | 13.3 ± 0.9 | 21.0 ± 0.9 | 83.9 ± 2.2 |
| LW × YC | 1.44 ± 0.08 | 3.66 ± 0.24 | 6.38 ± 0.43 | 13.8 ± 0.9 | 21.5 ± 0.9 | 88.4 ± 2.1 |
| CW × YL | 1.41 ± 0.06 | 3.83 ± 0.16 | 6.86 ± 0.29 | 15.0 ± 0.6 | 23.3 ± 0.5 | 90.6 ± 1.2 |
| CW × LY | 1.44 ± 0.08 | 3.71 ± 0.23 | 6.63 ± 0.43 | 14.5 ± 0.9 | 21.7 ± 0.9 | 88.0 ± 2.1 |
| CL × YW | 1.47 ± 0.08 | 4.03 ± 0.24 | 6.98 ± 0.43 | 14.9 ± 0.9 | 22.0 ± 0.8 | 87.8 ± 2.0 |
| CL × WY | 1.58 ± 0.09 | 3.92 ± 0.26 | 7.23 ± 0.48 | 15.1 ± 1.0 | 22.8 ± 1.0 | 88.9 ± 2.5 |
| CY × LW | 1.60 ± 0.10 | 4.49 ± 0.28 | 8.52 ± 0.51 | 17.9 ± 1.0 | 25.0 ± 1.1 | 95.0 ± 2.7 |
| CY × WL | 1.46 ± 0.08 | 4.19 ± 0.23 | 7.51 ± 0.42 | 15.3 ± 0.9 | 22.8 ± 0.8 | 91.3 ± 2.0 |
| $F_2$[b] | 1.24 ± 0.07 | 3.42 ± 0.19 | 6.45 ± 0.35 | 14.6 ± 0.7 | 21.8 ± 0.7 | 88.4 ± 1.6 |
| $F_2$[c] | 1.32 ± 0.07 | 3.55 ± 0.19 | 6.42 ± 0.35 | 14.2 ± 0.7 | 22.0 ± 0.6 | 86.7 ± 1.5 |
| $F_3$ | 1.35 ± 0.04 | 3.63 ± 0.12 | 6.59 ± 0.22 | 14.6 ± 0.5 | 22.2 ± 0.2 | 87.5 ± 0.5 |

[a]Y = Yorkshire, L = Landrace, W = Large White, and C = Chester White. The first letter indicates breed of sire, and the second letter indicates breed of dam. $F_3$, $F_4$, $F_5$, and $F_6$ were pooled. Progeny of reciprocal two-breed dams were classified separately to account for maternal grandam breed effects, but progeny of reciprocal two-breed cross sires were pooled.
[b]$F_2$ animals with YL maternal grandams.
[c]$F_2$ animals with CW maternal grandams.

**Appendix Table 2**. Least-squares means and standard errors of breed types for weights (kg) in Experiment 2

| Breed type[a] | Birth | 14 d | 28 d | 56 d | 70 d | 154 d |
|---|---|---|---|---|---|---|
| H × H | 1.05 ± 0.08 | 3.12 ± 0.18 | 5.88 ± 0.34 | 10.4 ± 0.7 | 15.5 ± 0.8 | 74.6 ± 0.8 |
| D × D | 1.07 ± 0.08 | 3.00 ± 0.18 | 5.36 ± 0.34 | 10.7 ± 0.7 | 15.9 ± 0.8 | 73.5 ± 0.8 |
| P × P | 1.06 ± 0.08 | 3.11 ± 0.18 | 5.57 ± 0.34 | 10.9 ± 0.7 | 15.4 ± 0.8 | 68.8 ± 0.8 |
| S × S | 1.21 ± 0.08 | 3.39 ± 0.19 | 6.19 ± 0.34 | 13.6 ± 0.7 | 20.0 ± 0.8 | 83.7 ± 0.8 |
| H × D | 1.11 ± 0.09 | 3.08 ± 0.25 | 5.24 ± 0.47 | 11.8 ± 0.9 | 18.6 ± 1.1 | 84.1 ± 2.4 |
| D × H | 1.06 ± 0.10 | 3.30 ± 0.30 | 5.94 ± 0.56 | 12.1 ± 1.1 | 18.4 ± 1.3 | 85.3 ± 3.1 |
| P × S | 1.26 ± 0.10 | 3.94 ± 0.28 | 7.23 ± 0.51 | 15.2 ± 1.0 | 22.1 ± 1.2 | 89.4 ± 2.7 |
| S × P | 1.18 ± 0.10 | 3.86 ± 0.29 | 6.78 ± 0.54 | 15.6 ± 1.1 | 20.9 ± 1.2 | 87.7 ± 2.7 |
| S × H | 1.11 ± 0.09 | 3.61 ± 0.23 | 6.51 ± 0.42 | 13.2 ± 0.8 | 19.6 ± 1.0 | 85.2 ± 1.8 |
| H × S | 1.33 ± 0.09 | 4.13 ± 0.23 | 7.36 ± 0.43 | 15.0 ± 0.9 | 22.1 ± 1.0 | 92.2 ± 1.9 |
| S × D | 1.23 ± 0.10 | 3.33 ± 0.27 | 5.81 ± 0.49 | 12.3 ± 1.0 | 18.4 ± 1.2 | 81.2 ± 2.5 |
| D × S | 1.32 ± 0.10 | 3.91 ± 0.28 | 7.41 ± 0.52 | 15.1 ± 1.0 | 22.2 ± 1.2 | 93.5 ± 2.8 |
| P × D | 1.27 ± 0.08 | 3.59 ± 0.22 | 6.32 ± 0.40 | 13.6 ± 0.8 | 20.2 ± 0.9 | 83.3 ± 1.6 |
| D × P | 1.17 ± 0.09 | 3.65 ± 0.24 | 6.64 ± 0.44 | 13.2 ± 0.9 | 19.0 ± 1.0 | 84.2 ± 2.0 |
| P × H | 1.04 ± 0.11 | 3.32 ± 0.31 | 6.12 ± 0.56 | 13.0 ± 1.1 | 18.3 ± 1.3 | 79.7 ± 3.1 |
| H × P | 1.22 ± 0.10 | 3.72 ± 0.28 | 6.63 ± 0.52 | 12.7 ± 1.0 | 19.2 ± 1.2 | 86.0 ± 2.7 |
| SH × PD | 1.22 ± 0.08 | 3.62 ± 0.21 | 6.16 ± 0.40 | 13.3 ± 0.8 | 20.2 ± 0.9 | 86.4 ± 1.6 |

| | | | | | | |
|---|---|---|---|---|---|---|
| SH × DP | 1.24 ± 0.08 | 3.47 ± 0.22 | 5.91 ± 0.40 | 13.1 ± 0.8 | 19.4 ± 0.9 | 86.2 ± 1.7 |
| PD × SH | 1.18 ± 0.09 | 3.56 ± 0.23 | 6.35 ± 0.42 | 13.5 ± 0.8 | 19.3 ± 1.0 | 85.0 ± 1.9 |
| PD × HS | 1.12 ± 0.09 | 3.22 ± 0.22 | 5.75 ± 0.41 | 12.9 ± 0.8 | 19.4 ± 1.0 | 85.8 ± 1.7 |
| PH × SD | 1.37 ± 0.10 | 3.55 ± 0.27 | 6.82 ± 0.49 | 13.8 ± 1.0 | 19.8 ± 1.2 | 85.0 ± 2.6 |
| PH × DS | 1.25 ± 0.09 | 3.53 ± 0.25 | 6.58 ± 0.47 | 13.7 ± 0.9 | 20.4 ± 1.2 | 87.2 ± 2.5 |
| SD × PH | 1.21 ± 0.10 | 3.80 ± 0.26 | 6.96 ± 0.48 | 13.5 ± 1.0 | 20.8 ± 1.2 | 87.2 ± 2.6 |
| SD × HP | 1.15 ± 0.09 | 3.57 ± 0.25 | 6.36 ± 0.47 | 13.5 ± 0.9 | 20.1 ± 1.1 | 88.0 ± 2.4 |
| HD × SP | 1.38 ± 0.10 | 4.30 ± 0.27 | 7.60 ± 0.50 | 15.6 ± 1.0 | 22.8 ± 1.2 | 89.0 ± 2.7 |
| HD × PS | 1.41 ± 0.09 | 4.11 ± 0.25 | 6.87 ± 0.47 | 14.3 ± 0.9 | 20.7 ± 1.1 | 88.6 ± 2.3 |
| SP × DH | 1.12 ± 0.09 | 3.42 ± 0.26 | 6.09 ± 0.47 | 13.7 ± 0.9 | 19.6 ± 1.2 | 86.2 ± 2.6 |
| SP × HD | 1.12 ± 0.10 | 3.55 ± 0.26 | 6.25 ± 0.48 | 14.4 ± 0.9 | 21.7 ± 1.2 | 86.0 ± 2.4 |
| $F_2$[b] | 1.12 ± 0.09 | 3.07 ± 0.25 | 5.38 ± 0.46 | 11.4 ± 0.9 | 18.2 ± 1.1 | 81.6 ± 2.1 |
| $F_2$[c] | 1.17 ± 0.09 | 3.39 ± 0.23 | 6.04 ± 0.43 | 12.8 ± 0.9 | 18.9 ± 1.0 | 85.0 ± 1.8 |
| $F_3$ | 1.22 ± 0.07 | 3.57 ± 0.18 | 6.46 ± 0.33 | 13.2 ± 0.7 | 19.2 ± 0.8 | 83.5 ± 0.6 |

[a]H = Hampshire, D = Duroc, P = Pietrain, and S = Spot. The first letter indicates breed of sire, and the second letter indicates breed of dam. $F_3$, $F_4$, $F_5$, and $F_6$ were pooled. Progeny of reciprocal two-breed dams were classified separately to account for maternal grandam breed effects, but progeny of reciprocal two-breed cross sires were pooled.
[b]$F_2$ animals with SH or HS maternal grandams.
[c]$F_2$ animals with DP or PD maternal grandams.

**Appendix Table 3**. Least-squares means and standard errors of breed types for carcass traits in Experiment 1

| Breed type[a] | Ultrasonic backfat, mm | Carcass backfat[b], mm | Carcass length, cm | Loin muscle area, $cm^2$ |
|---|---|---|---|---|
| Y × Y | 18.3 ± 0.3 | 38.4 ± 0.6 | 77.7 ± 0.3 | 33.9 ± 0.5 |
| L × L | 18.1 ± 0.2 | 33.8 ± 0.5 | 81.8 ± 0.3 | 29.7 ± 0.5 |
| W × W | 17.2 ± 0.3 | 36.0 ± 0.6 | 80.2 ± 0.3 | 31.3 ± 0.5 |
| C × C | 19.7 ± 0.4 | 36.4 ± 0.8 | 77.2 ± 0.4 | 31.9 ± 0.7 |
| Y × L | 18.0 ± 0.4 | 35.5 ± 1.0 | 80.2 ± 0.5 | 33.0 ± 1.0 |
| L × Y | 20.6 ± 0.9 | 37.4 ± 1.8 | 78.7 ± 0.9 | 32.8 ± 1.7 |
| Y × W | 18.6 ± 0.9 | 35.5 ± 1.9 | 79.1 ± 0.9 | 33.8 ± 1.8 |
| W × Y | 17.9 ± 0.9 | 39.4 ± 2.0 | 79.5 ± 1.0 | 30.1 ± 1.9 |
| L × W | 18.4 ± 1.1 | 32.7 ± 1.9 | 81.7 ± 0.9 | 32.1 ± 1.8 |
| W × L | 18.6 ± 1.1 | 35.3 ± 2.2 | 81.1 ± 1.1 | 29.3 ± 2.1 |
| W × C | 20.8 ± 0.9 | 40.2 ± 1.8 | 78.3 ± 0.9 | 30.8 ± 1.7 |
| C × L | 19.3 ± 1.0 | 35.0 ± 1.9 | 79.7 ± 0.9 | 34.8 ± 1.8 |
| L × C | 20.7 ± 1.1 | 38.0 ± 2.0 | 79.2 ± 1.2 | 29.9 ± 2.3 |
| C × Y | 19.5 ± 0.9 | 34.6 ± 2.5 | 77.5 ± 1.2 | 36.3 ± 2.3 |
| Y × C | 21.4 ± 1.1 | 41.7 ± 2.1 | 78.5 ± 1.0 | 29.7 ± 1.9 |
| C × W | 17.5 ± 0.5 | 32.8 ± 1.1 | 79.4 ± 0.5 | 34.8 ± 1.0 |
| YL × CW | 19.3 ± 0.5 | 36.5 ± 1.2 | 79.3 ± 0.6 | 31.5 ± 1.1 |
| YL × WC | 18.2 ± 1.1 | 37.3 ± 1.8 | 78.9 ± 0.9 | 32.3 ± 1.7 |
| YW × CL | 21.1 ± 1.1 | 41.6 ± 2.0 | 78.4 ± 1.0 | 35.1 ± 1.9 |
| YW × LC | 19.0 ± 1.0 | 36.8 ± 1.8 | 79.6 ± 0.9 | 32.2 ± 1.7 |
| LW × CY | 17.1 ± 0.9 | 37.1 ± 1.8 | 78.5 ± 0.9 | 34.5 ± 1.7 |
| LW × YC | 18.2 ± 1.0 | 39.5 ± 1.9 | 79.4 ± 0.9 | 31.4 ± 1.8 |
| CW × YL | 18.2 ± 0.5 | 35.5 ± 1.1 | 79.5 ± 0.5 | 34.5 ± 1.0 |
| CW × LY | 20.2 ± 0.9 | 40.1 ± 1.8 | 78.4 ± 0.8 | 33.1 ± 1.7 |
| CL × YW | 17.8 ± 1.0 | 35.2 ± 1.7 | 79.2 ± 0.8 | 35.8 ± 1.6 |
| CL × WY | 20.0 ± 1.3 | 38.1 ± 2.1 | 78.4 ± 1.0 | 34.4 ± 1.9 |
| CY × LW | 16.2 ± 3.0 | 34.7 ± 3.5 | 80.4 ± 1.7 | 33.0 ± 3.3 |
| CY × WL | 18.8 ± 0.9 | 35.4 ± 1.6 | 80.3 ± 0.8 | 32.3 ± 1.5 |
| $F_2$[c] | 17.9 ± 0.6 | 35.6 ± 1.4 | 79.0 ± 0.7 | 31.5 ± 1.3 |
| $F_2$[d] | 18.3 ± 0.6 | 35.8 ± 1.4 | 78.6 ± 0.7 | 31.0 ± 1.3 |
| $F_3$ | 18.5 ± 0.2 | 36.8 ± 0.4 | 79.7 ± 0.2 | 30.4 ± 0.4 |

[a]Y = Yorkshire, L = Landrace, W = Large White, and C = Chester White. The first letter indicates breed of sire, and the second letter indicates breed of dam. $F_3$, $F_4$, $F_5$, and $F_6$ were pooled. Progeny of reciprocal two-breed dams were classified separately to account for maternal grandam breed effects, but progeny of reciprocal two-breed cross sires were pooled.
[b]Carcass backfat was averaged across measurements taken at the first rib, last rib, and last lumbar.
[c]$F_2$ animals with YL maternal grandams.
[d]$F_2$ animals with CW maternal grandams.

**Appendix Table 4**. Least-squares means and standard errors of breed types for carcass traits in Experiment 2

| Breed type[a] | Ultrasonic backfat, mm | Carcass backfat[b], mm | Carcass length, cm | Loin muscle area, $cm^2$ |
|---|---|---|---|---|
| H × H | 17.5 ± 0.2 | 32.1 ± 0.6 | 77.7 ± 0.3 | 36.3 ± 0.7 |
| D × D | 21.2 ± 0.2 | 36.9 ± 0.6 | 77.4 ± 0.3 | 31.4 ± 0.7 |
| P × P | 18.0 ± 0.2 | 37.7 ± 0.8 | 72.7 ± 0.4 | 38.0 ± 0.8 |
| S × S | 17.4 ± 0.2 | 35.4 ± 0.7 | 78.7 ± 0.4 | 34.0 ± 0.8 |
| H × D | 18.0 ± 0.7 | 33.9 ± 2.2 | 78.9 ± 1.1 | 35.3 ± 2.3 |
| D × H | 18.6 ± 0.9 | 37.9 ± 2.5 | 76.7 ± 1.3 | 34.6 ± 2.7 |
| P × S | 18.0 ± 0.8 | 35.3 ± 2.8 | 75.7 ± 1.4 | 33.1 ± 3.0 |
| S × P | 16.3 ± 0.8 | 32.6 ± 2.1 | 76.6 ± 1.1 | 35.5 ± 2.2 |
| S × H | 18.9 ± 0.5 | 35.2 ± 1.8 | 79.0 ± 0.9 | 36.9 ± 1.9 |
| H × S | 16.2 ± 0.5 | 30.7 ± 2.1 | 79.5 ± 1.1 | 36.4 ± 2.2 |
| S × D | 19.0 ± 0.8 | 37.5 ± 2.0 | 79.7 ± 1.1 | 33.4 ± 2.2 |
| D × S | 16.6 ± 0.9 | 32.0 ± 2.5 | 79.4 ± 1.3 | 39.9 ± 2.7 |
| P × D | 20.4 ± 0.4 | 39.0 ± 1.2 | 76.1 ± 0.6 | 32.6 ± 1.3 |
| D × P | 18.2 ± 0.6 | 35.1 ± 1.8 | 75.0 ± 0.9 | 38.7 ± 2.0 |
| P × H | 18.2 ± 0.9 | 37.7 ± 2.4 | 75.2 ± 1.2 | 36.0 ± 2.6 |
| H × P | 16.1 ± 0.8 | 32.8 ± 1.9 | 75.1 ± 1.0 | 41.2 ± 2.1 |
| SH × PD | 18.7 ± 0.5 | 35.0 ± 1.3 | 76.6 ± 0.6 | 36.9 ± 1.3 |
| SH × DP | 19.7 ± 0.5 | 35.7 ± 1.2 | 76.4 ± 0.6 | 34.1 ± 1.3 |
| PD × SH | 17.6 ± 0.6 | 34.6 ± 1.9 | 76.5 ± 1.0 | 35.5 ± 2.0 |
| PD × HS | 18.4 ± 0.5 | 33.5 ± 1.2 | 76.6 ± 0.6 | 36.6 ± 1.3 |
| PH × SD | 17.4 ± 0.8 | 36.7 ± 2.2 | 75.8 ± 1.2 | 35.0 ± 2.4 |
| PH × DS | 16.8 ± 0.8 | 32.1 ± 2.4 | 79.1 ± 1.2 | 36.4 ± 2.6 |
| SD × PH | 17.9 ± 0.9 | 32.0 ± 2.1 | 76.9 ± 1.1 | 34.0 ± 2.3 |
| SD × HP | 19.6 ± 0.8 | 36.0 ± 1.7 | 76.9 ± 0.9 | 35.7 ± 1.9 |
| HD × SP | 17.6 ± 0.9 | 33.2 ± 2.2 | 78.7 ± 1.2 | 35.5 ± 2.4 |
| HD × PS | 17.4 ± 0.8 | 32.6 ± 1.7 | 76.4 ± 0.9 | 38.9 ± 1.8 |
| SP × DH | 19.0 ± 0.8 | 34.9 ± 2.0 | 78.1 ± 1.0 | 38.8 ± 2.2 |
| SP × HD | 19.1 ± 0.8 | 34.2 ± 1.9 | 77.5 ± 1.0 | 34.4 ± 2.1 |
| $F_2$[c] | 18.4 ± 0.6 | 33.7 ± 1.7 | 74.5 ± 0.9 | 35.7 ± 1.8 |
| $F_2$[d] | 18.7 ± 0.6 | 37.1 ± 1.5 | 74.6 ± 0.8 | 33.7 ± 1.6 |
| $F_3$ | 19.0 ± 0.2 | 34.8 ± 0.5 | 77.4 ± 0.2 | 34.4 ± 0.5 |

[a]H = Hampshire, D = Duroc, P = Pietrain, and S = Spot. The first letter indicates breed of sire, and the second letter indicates breed of dam. $F_3$, $F_4$, $F_5$, and $F_6$ were pooled. Progeny of reciprocal two-breed dams were classified separately to account for maternal grandam breed effects, but progeny of reciprocal two-breed cross sires were pooled.

[b]Carcass backfat was averaged across measurements taken at the first rib, last rib, and last lumbar.

[c]$F_2$ animals with SH or HS maternal grandams.

[d]$F_2$ animals with DP or PD maternal grandams.

**Appendix Table 5**. Least-squares means and standard errors of breed types for ADG and ADFI in Experiment 1

| | ADG, g/d | | | | ADFI, kg/d |
|---|---|---|---|---|---|
| Breed type[a] | Birth to 14 d | 14 to 28 d | 28 to 56 d | 70 to 154 d | 70 to 154 d |
| Y × Y | 142 ± 8 | 201 ± 10 | 221 ± 12 | 722 ± 6 | 2.17 ± 0.03 |
| L × L | 140 ± 7 | 187 ± 10 | 248 ± 12 | 749 ± 6 | 2.31 ± 0.03 |
| W × W | 145 ± 8 | 200 ± 10 | 248 ± 12 | 775 ± 6 | 2.32 ± 0.04 |
| C × C | 125 ± 8 | 197 ± 10 | 227 ± 12 | 693 ± 6 | 2.13 ± 0.04 |
| Y × L | 151 ± 9 | 193 ± 12 | 285 ± 15 | 788 ± 10 | 2.43 ± 0.06 |
| L × Y | 163 ± 15 | 217 ± 19 | 264 ± 23 | 804 ± 20 | 2.58 ± 0.12 |
| Y × W | 199 ± 14 | 235 ± 19 | 262 ± 23 | 798 ± 20 | 2.45 ± 0.13 |
| W × Y | 152 ± 15 | 192 ± 20 | 274 ± 24 | 763 ± 21 | 2.35 ± 0.13 |
| L × W | 185 ± 15 | 236 ± 19 | 317 ± 24 | 838 ± 21 | 2.49 ± 0.12 |
| W × L | 154 ± 14 | 210 ± 19 | 322 ± 23 | 806 ± 20 | 2.56 ± 0.13 |
| W × C | 158 ± 15 | 190 ± 20 | 321 ± 24 | 796 ± 21 | 2.63 ± 0.12 |
| C × L | 153 ± 15 | 232 ± 20 | 305 ± 24 | 792 ± 21 | 2.53 ± 0.12 |
| L × C | 185 ± 14 | 210 ± 19 | 306 ± 23 | 781 ± 20 | 2.55 ± 0.15 |
| C × Y | 179 ± 14 | 204 ± 19 | 275 ± 23 | 762 ± 20 | 2.46 ± 0.14 |
| Y × C | 155 ± 17 | 205 ± 22 | 251 ± 27 | 774 ± 23 | 2.90 ± 0.14 |
| C × W | 153 ± 10 | 212 ± 13 | 280 ± 16 | 818 ± 11 | 2.41 ± 0.07 |
| YL × CW | 150 ± 10 | 202 ± 13 | 284 ± 15 | 790 ± 11 | 2.36 ± 0.07 |

| | | | | | |
|---|---|---|---|---|---|
| YL × WC | 177 ± 15 | 220 ± 19 | 322 ± 23 | 814 ± 20 | 2.64 ± 0.12 |
| YW × CL | 160 ± 14 | 205 ± 18 | 322 ± 22 | 821 ± 19 | 2.46 ± 0.13 |
| YW × LC | 168 ± 13 | 225 ± 17 | 315 ± 21 | 781 ± 19 | 2.50 ± 0.12 |
| LW × CY | 140 ± 14 | 183 ± 18 | 266 ± 22 | 753 ± 20 | 2.35 ± 0.12 |
| LW × YC | 160 ± 14 | 192 ± 18 | 266 ± 22 | 802 ± 19 | 2.56 ± 0.12 |
| CW × YL | 173 ± 9 | 216 ± 12 | 291 ± 15 | 806 ± 11 | 2.47 ± 0.07 |
| CW × LY | 163 ± 14 | 209 ± 18 | 281 ± 22 | 797 ± 19 | 2.55 ± 0.12 |
| CL × YW | 186 ± 14 | 212 ± 18 | 281 ± 22 | 793 ± 18 | 2.57 ± 0.11 |
| CL × WY | 167 ± 16 | 237 ± 20 | 282 ± 25 | 788 ± 23 | 2.48 ± 0.14 |
| CY × LW | 208 ± 17 | 289 ± 22 | 337 ± 26 | 845 ± 25 | 2.62 ± 0.19 |
| CY × WL | 192 ± 14 | 238 ± 18 | 274 ± 22 | 824 ± 19 | 2.52 ± 0.12 |
| $F_2$[b] | 153 ± 11 | 216 ± 15 | 290 ± 18 | 798 ± 14 | 2.48 ± 0.09 |
| $F_2$[c] | 158 ± 11 | 205 ± 15 | 275 ± 18 | 777 ± 14 | 2.47 ± 0.09 |
| $F_3$ | 162 ± 7 | 211 ± 9 | 285 ± 12 | 782 ± 5 | 2.45 ± 0.03 |

[a]Y = Yorkshire, L = Landrace, W = Large White, and C = Chester White. The first letter indicates breed of sire, and the second letter indicates breed of dam. $F_3$, $F_4$, $F_5$, and $F_6$ were pooled. Progeny of reciprocal two-breed dams were classified separately to account for maternal grandam breed effects, but progeny of reciprocal two-breed cross sires were pooled.
[b]$F_2$ animals with YL maternal grandams.
[c]$F_2$ animals with CW maternal grandams.

**Appendix Table 6**. Least-squares means and standard errors of breed types for ADG and ADFI in Experiment 2

| | ADG, g/d | | | | ADFI, kg/d |
|---|---|---|---|---|---|
| Breed type[a] | Birth to 14 d | 14 to 28 d | 28 to 56 d | 70 to 154 d | 70 to 154 d |
| H × H | 135 ± 11 | 196 ± 15 | 161 ± 17 | 699 ± 7 | 2.07 ± 0.04 |
| D × D | 124 ± 11 | 167 ± 15 | 190 ± 17 | 681 ± 7 | 2.13 ± 0.04 |
| P × P | 135 ± 11 | 174 ± 15 | 186 ± 17 | 632 ± 7 | 1.83 ± 0.05 |
| S × S | 142 ± 11 | 200 ± 15 | 263 ± 17 | 756 ± 7 | 2.51 ± 0.05 |
| H × D | 128 ± 15 | 157 ± 20 | 232 ± 23 | 774 ± 23 | 2.57 ± 0.17 |
| D × H | 142 ± 18 | 190 ± 24 | 219 ± 28 | 790 ± 29 | 2.37 ± 0.19 |
| P × S | 174 ± 17 | 237 ± 22 | 284 ± 26 | 793 ± 26 | 2.44 ± 0.20 |
| S × P | 180 ± 18 | 211 ± 23 | 315 ± 27 | 789 ± 25 | 2.36 ± 0.16 |
| S × H | 165 ± 14 | 210 ± 18 | 238 ± 21 | 775 ± 17 | 2.57 ± 0.12 |
| H × S | 180 ± 14 | 233 ± 19 | 273 ± 21 | 827 ± 18 | 2.54 ± 0.13 |
| S × D | 138 ± 16 | 179 ± 21 | 231 ± 24 | 741 ± 24 | 3.12 ± 0.16 |
| D × S | 174 ± 17 | 252 ± 22 | 276 ± 26 | 837 ± 27 | 3.02 ± 0.18 |
| P × D | 155 ± 13 | 196 ± 17 | 261 ± 20 | 745 ± 15 | 2.42 ± 0.09 |
| D × P | 164 ± 14 | 215 ± 19 | 232 ± 22 | 767 ± 19 | 2.77 ± 0.12 |
| P × H | 153 ± 19 | 201 ± 25 | 243 ± 28 | 724 ± 29 | 2.56 ± 0.19 |
| H × P | 170 ± 17 | 210 ± 23 | 214 ± 26 | 792 ± 26 | 2.31 ± 0.16 |
| SH × PD | 157 ± 13 | 183 ± 17 | 256 ± 20 | 783 ± 15 | 2.55 ± 0.10 |
| SH × DP | 148 ± 13 | 175 ± 17 | 257 ± 20 | 789 ± 16 | 2.71 ± 0.10 |
| PD × SH | 154 ± 14 | 201 ± 18 | 253 ± 21 | 779 ± 18 | 2.49 ± 0.16 |
| PD × HS | 138 ± 13 | 182 ± 18 | 255 ± 20 | 784 ± 16 | 2.52 ± 0.10 |
| PH × SD | 143 ± 16 | 188 ± 21 | 271 ± 25 | 772 ± 24 | 2.26 ± 0.17 |
| PH × DS | 151 ± 15 | 221 ± 20 | 253 ± 23 | 790 ± 24 | 2.62 ± 0.18 |
| SD × PH | 172 ± 16 | 227 ± 21 | 232 ± 24 | 786 ± 25 | 2.50 ± 0.18 |
| SD × HP | 158 ± 15 | 201 ± 20 | 255 ± 23 | 804 ± 22 | 2.59 ± 0.14 |
| HD × SP | 197 ± 16 | 234 ± 22 | 284 ± 25 | 784 ± 25 | 2.42 ± 0.18 |
| HD × PS | 180 ± 15 | 199 ± 20 | 264 ± 23 | 805 ± 22 | 2.56 ± 0.14 |
| SP × DH | 154 ± 16 | 193 ± 21 | 272 ± 24 | 785 ± 24 | 2.68 ± 0.16 |
| SP × HD | 159 ± 16 | 195 ± 21 | 289 ± 24 | 763 ± 23 | 2.52 ± 0.16 |
| $F_2$[b] | 126 ± 15 | 164 ± 20 | 214 ± 23 | 750 ± 20 | 2.54 ± 0.12 |
| $F_2$[c] | 144 ± 14 | 186 ± 19 | 239 ± 22 | 783 ± 17 | 2.68 ± 0.10 |
| $F_3$ | 155 ± 11 | 206 ± 14 | 239 ± 17 | 761 ± 6 | 2.59 ± 0.03 |

[a]H = Hampshire, D = Duroc, P = Pietrain, and S = Spot. The first letter indicates breed of sire, and the second letter indicates breed of dam. $F_3$, $F_4$, $F_5$, and $F_6$ were pooled. Progeny of reciprocal two-breed dams were classified separately to account for maternal grandam breed effects, but progeny of reciprocal two-breed cross sires were pooled.
[b]$F_2$ animals with SH or HS maternal grandams.
[c]$F_2$ animals with DP or PD maternal grandams.